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Upper Cretaceous ammonites from the Calabar region, south-east Nigeria

P. M. P. Zaborski

Geology series Vol 39 No 1 27 June 1985

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Upper Cretaceous ammonites from the Calabar region, south-east Nigeria

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Contents

Synopsis 2
Introduction 2
Systematic descriptions 5
  Family Gaudryceratidae Spath 5
    Genus *Anagaudryceras* Shimizu 5
      Anagaudryceras involvulum (Stoliczka) 7
    Genus *Gaudryceras* Grossouvre 8
      Gaudryceras beantalyense Collignon 8
      Gaudryceras varicostatum van Hoepen 10
  Family Turrilitidae Meek 10
   Subfamily Turrilitinae Gill 10
    Genus *Turrilites* Lamarck 10
     Subgenus *Turrilites* Lamarck 10
      Turrilites (*Turrilites*) *scheuchzerianus* Bosc 10
      Turrilites (*Turrilites*) *costatus* Lamarck 10
      Turrilites (*Turrilites*) *acutus* Passy 11
   Subfamily Nostoceratinae Hyatt 11
    Genus *Pseudoxybeloceras* Wright & Matsumoto 11
     Subgenus *Parasolenoceras* Collignon 11
      Pseudoxybeloceras (*Parasolenoceras*) aff. *splendens* Collignon 13
    Genus *Didymoceras* Hyatt 14
      Didymoceras aff. *hornbyense* (Whiteaves) 14
      Didymoceras aff. *cheyennense* (Meek & Hayden) 17
  Family Desmoceratidae Zittel 17
   Subfamily Puzosiinae Spath 17
    Genus *Puzosia* Bayle 17
     Subgenus *Anapuzosia* Matsumoto 17
      Puzosia (*Anapuzosia*) cf. *dibleyi* (Spath) 17
  Family Pachydiscidae Spath 19
    Genus *Pachydiscus* Zittel 19
     Subgenus *Pachydiscus* Zittel 19
      Pachydiscus (*Pachydiscus*) *egertoni* (Forbes) 19
      Pachydiscus (*Pachydiscus*) *dossantosi* (Maury) 20
  Family Forbesiceratidae Wright 22
    Genus *Forbesiceras* Kossmat 22
      Forbesiceras subobtectum (Stoliczka) 22
      Forbesiceras obtectum (Sharpe) 22
  Family Acanthoceratidae Grossouvre 26
   Subfamily Mantelliceratinae Hyatt 26
    Genus *Sharpeiceras* Hyatt 26
      Sharpeiceras laticlavium (Sharpe) *nigeriense* subsp. nov. 26
    Genus *Acompsoceras* Hyatt 29
      Acompsoceras calabarense sp. nov. 29
      Acompsoceras aff. *renevieri* (Sharpe) 30

Bull. Br. Mus. nat. Hist. (Geol.) **39** (1): 1–72

Issued 27 June 1985

Genus *Pseudocalycoceras* Thomel 30
- *Pseudocalycoceras* cf. *haughi* (Pervinquière) 30

Genus *Calycoceras* Hyatt 32
- Subgenus *Newboldiceras* Thomel 32
  - *Calycoceras* (*Newboldiceras*) *annulatum* Collignon 32

Subfamily Acanthoceratinae Grossouvre 33
- Genus *Acanthoceras* Neumayr 33
  - *Acanthoceras robustum* Crick 33
  - *Acanthoceras amphibolum* Morrow 35
  - *Acanthoceras* sp. 38

Subfamily Euomphaloceratinae Cooper 39
- Genus *Euomphaloceras* Spath 39
  - *Euomphaloceras inerme* (Pervinquière) 40
  - *Euomphaloceras cunningtoni* (Sharpe) 42
    - *Euomphaloceras cunningtoni meridionale* (Stoliczka) 43
    - *Euomphaloceras cunningtoni cunningtoni* (Sharpe) 45
    - *Euomphaloceras cunningtoni alatum* subsp. nov. 49
- Genus *Kamerunoceras* Reyment 51
  - *Kamerunoceras tinrhertense* Collignon 51

Family Coilopoceratidae Hyatt 53
- Genus *Coilopoceras* Hyatt 53
  - *Coilopoceras* aff. *newelli* Benavides-Cáceres 55

Family Sphenodiscidae Hyatt 57
- Genus *Sphenodiscus* Meek 57
  - *Sphenodiscus lobatus* (Tuomey) *costatus* Zaborski 57

Correlation and palaeogeography 58

Acknowledgements 63

References 63

Note added in proof 69

Index 70

Synopsis

Ammonites of Cenomanian, Turonian, Campanian and Maastrichtian age are described from the Calabar region of south-eastern Nigeria. The Albian–Turonian Odukpani Formation yields Lower Cenomanian ammonites including *Sharpeiceras laticlavium nigeriense* subsp. nov. and *Acompsoceras calabarense* sp. nov., but these faunas are, as yet, poorly known. Middle Cenomanian forms are of a dominantly north-west European character with species of *Anagaudryceras, Turrilites, Forbesiceras* and *Euomphaloceras* in common. The *Euomphaloceras cunningtoni* group is represented by the stratigraphically successive subspecies *E. cunningtoni meridionale* (Stoliczka), *E. cunningtoni cunningtoni* (Sharpe) and *E. cunningtoni alatum* subsp. nov. Also present is the typically North American late Middle Cenomanian species *Acanthoceras amphibolum* Morrow. The genus *Pseudocalycoceras* indicates the presence of Upper Cenomanian, but most of this substage, as well as the uppermost part of the Middle Cenomanian, is probably absent. The Turonian part of the Odukpani Formation yields *Kamerunoceras* and *Coilopoceras.* The overlying Nkporo Shale contains an Upper Campanian fauna at its base, with species of *Gaudryceras, Pseudoxybeloceras* (*Parasolenoceras*), *Didymoceras, Pachydiscus, Libycoceras* and *Sphenodiscus*, while its upper part, with *Gaudryceras, Pachydiscus* and *Sphenodiscus*, is of Lower Maastrichtian age.

The Cenomanian forms provide a palaeobiogeographical link between the north-west European and Angolan faunas, indicating that faunal interchange between the North and South Atlantic Ocean was possible.

Introduction

To the north of Calabar in south-eastern Nigeria, a basement block, the Oban Massif, is flanked on its southern side by a series of Cretaceous sediments. This region is of particular interest as it contains the most complete sequence of marine Cenomanian strata exposed in Nigeria and, except for Angola, in any part of west coastal Africa. Although the late

Cenomanian saw the onset of a transgression that was to culminate during the early Turonian, Cenomanian environments in Nigeria are thought to have been mainly regressive. Marine uppermost Cenomanian containing *Euomphaloceras septemseriatum* (Cragin) occurs in the middle Benue Valley of central Nigeria (Offodile 1976, Offodile & Reyment 1976) and faunas from the north-east of the country, with *Metengonoceras dumbli* (Cragin) and diverse vascoceratids (Barber 1957), are at least partly of Cenomanian age (see also Hancock & Kennedy 1981: 537). Otherwise, marine Cenomanian is known only from the Calabar region where the Odukpani Formation (Reyment 1955, 1956, 1965) includes Middle and Lower Cenomanian. Separated from the Precambrian basement by a thick sequence of continental clastics (the Awi Formation, see Adeleye & Fayose 1978), the Odukpani Formation extends from the Albian at its base to the Turonian in its upper part. It consists of shales, calcareous shales and sandstones with occasional beds of limestone. A thick limestone close to the base of the formation is well exposed in a quarry at Mfamosing, north-east of Calabar (Fig. 2, inset); Förster (1978) and Förster & Scholz (1979) reported a diverse Upper Albian–Lower Cenomanian ammonite fauna from here. Reyment (1955, 1957) and Fayose (1977) have described ammonites from higher in the Odukpani Formation. In the Calabar region the Odukpani Formation is overlain unconformably by the Upper Campanian–Lower Maastrichtian Nkporo Shale which, although probably only partly of marine origin, also contains ammonites at certain levels. The succeeding sediments belong to the continental late Tertiary Benin Formation.

The Odukpani Formation and Nkporo Shale are well exposed in road cuttings north-west of Calabar (Figs 1, 2), where the material described here was collected. Both formations have a gentle regional dip to the south-west. The lower part of the Odukpani Formation is, however, affected by broad folds trending NE–SW, and faulting may also be present. Dips rarely exceed 10°. The exposed parts of the Odukpani Formation consist here mainly of grey shales, pyritic at the base but calcareous and including numerous thin limestones higher up. A well-developed limestone–shale sequence occurs close to the top of the formation and at its base are the remnants after dissolution of another prominent limestone horizon. The folding makes it difficult to estimate the thickness of the formation: Reyment (1965: 34) gave a thickness of about 1000 m (including the basal clastics of the Awi Formation) but this is perhaps an underestimate. The outcropping part of the Nkporo Shale is about 700 m thick, an account of this part of the section and its *Libycoceras* and *Sphenodiscus* fauna having been given by Zaborski (1982).

A full list of the ammonites collected in the present study (not necessarily in stratigraphical order) is given below. Apart from faunas 1 and 2, all are from cuttings on the Calabar–Ikot Ekpene road (Figs 1–2) and are localized according to their distances from Calabar using the mileposts as reference points. From the Odukpani Formation the following forms were obtained:

Fauna 1. Road cutting on the Calabar–Akamkpa road, 1·5 km north of the junction with the Calabar–Ikot Ekpene road: *Desmoceras* sp., *Sharpeiceras laticlavium nigeriense* subsp. nov., *Acompsoceras calabarense* sp. nov.

Fauna 2. Road cutting on the Calabar–Akamkpa road, 1 km north of the junction with the Calabar–Ikot Ekpene road: *Puzosia* sp., *Acompsoceras* aff. *renevieri* (Sharpe), *A.* aff. *essendiense* (Schlüter).

Fauna 3. 25·8 km from Calabar: *Forbesiceras* sp., indeterminate acanthoceratids.

Fauna 4. 27·9 km from Calabar: *Turrilites* (*T.*) *scheuchzerianus* Bosc, *T.* (*T.*) *costatus* Lamarck, *Forbesiceras subobtectum* (Stoliczka), *Euomphaloceras inerme* (Pervinquière), *E. cunningtoni meridionale* (Stoliczka).

Fauna 5. 28·3 km from Calabar: *Turrilites* (*T.*) *costatus* Lamarck, *Desmoceras* (*Pseudouhligella*) sp., *Euomphaloceras cunningtoni cunningtoni* (Sharpe).

Fauna 6. 29·3 km from Calabar: *Desmoceras* (*Pseudouhligella*) sp., *Forbesiceras obtectum* (Sharpe).

Fauna 7. 30·1 km from Calabar: *Desmoceras* (*Pseudouhligella*) sp., *Puzosia* (*Anapuzosia*) cf.

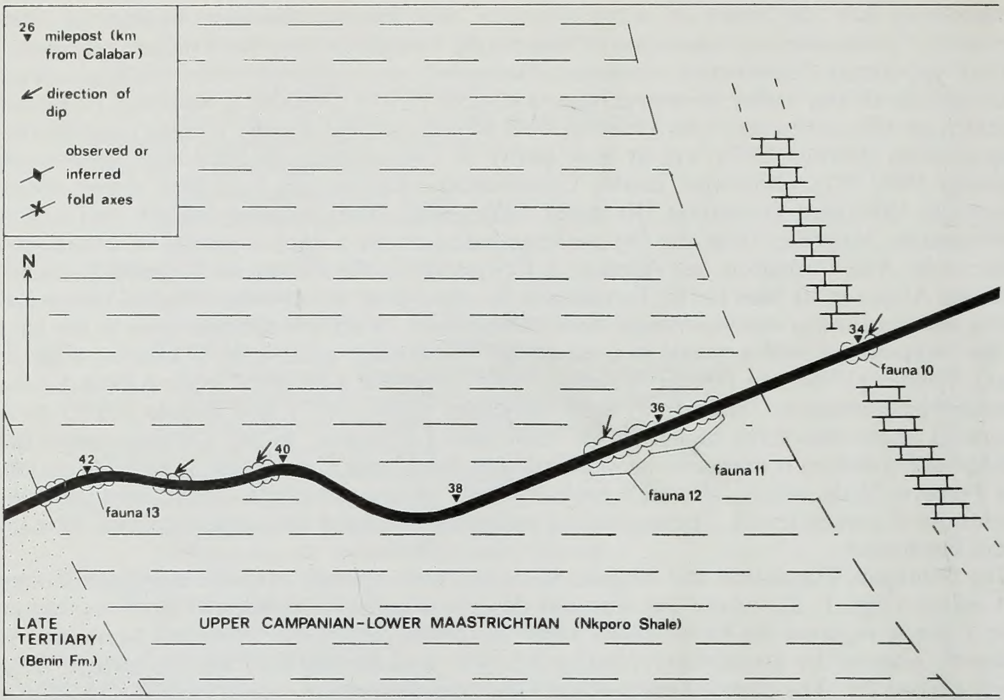

26 milepost (km from Calabar)
direction of dip
observed or inferred fold axes
N
34
fauna 10
36
fauna 11
fauna 12
38
40
42
fauna 13
LATE TERTIARY (Benin Fm.)
UPPER CAMPANIAN-LOWER MAASTRICHTIAN (Nkporo Shale)

Fig. 1 Map showing road section north of Calabar and localities of fossils mentioned in the text: western portion.

dibleyi (Spath), *Forbesiceras obtectum*?, *Acanthoceras amphibolum* Morrow, *Acanthoceras* sp.

Fauna 8. 30·3 km from Calabar: *Anagaudryceras involvulum* (Stoliczka), *Turrilites* (*T.*) *acutus* Passy, *Forbesiceras obtectum, Calycoceras* (*Newboldiceras*) *annulatum* Collignon, *Euomphaloceras cunningtoni alatum* subsp. nov.

Fauna 9. 32·2 km from Calabar: *Acanthoceras robustum* Crick, *Euomphaloceras cunningtoni alatum*?

Fauna 10. 34 km from Calabar: *Puzosia* sp., *Kamerunoceras tinrhertense* Collignon, *Coilopoceras* aff. *newelli* Benavides-Cáceres.

In addition, there is a single specimen of *Pseudocalycoceras* cf. *haughi* (Pervinquière), of which the exact horizon within the Odukpani Formation is unknown.

From the Nkporo Shale the full list is:

Fauna 11. 35·5–36·3 km from Calabar: *Gaudryceras varicostatum* van Hoepen, *Pseudoxybeloceras* (*Parasolenoceras*) aff. *splendens* Collignon, *Didymoceras* aff. *hornbyense* (Whiteaves), *D.* aff. *cheyennense* (Meek & Hayden), *Baculites* sp., *Pachydiscus* (*P.*) *egertoni* (Forbes), *Libycoceras afikpoense* Reyment, *Sphenodiscus lobatus lobatus* (Tuomey).

Fauna 12. 36·3–36·7 km from Calabar: *Nostoceras* sp., *Libycoceras crossense* Zaborski.

Fauna 13. 42 km from Calabar: *Gaudryceras beantalyense* Collignon, *Baculites* sp., *Pachydiscus* (*P.*) *dossantosi* (Maury), *Sphenodiscus lobatus costatus* Zaborski.

These faunas add considerably to knowledge of Nigerian ammonite sequences and allow a more detailed correlation to be made with other parts of the world than has hitherto been possible. They also provide some palaeogeographical information on the opening of the South Atlantic Ocean and the extent of the late Cretaceous transgression in western Africa and the Sahara.

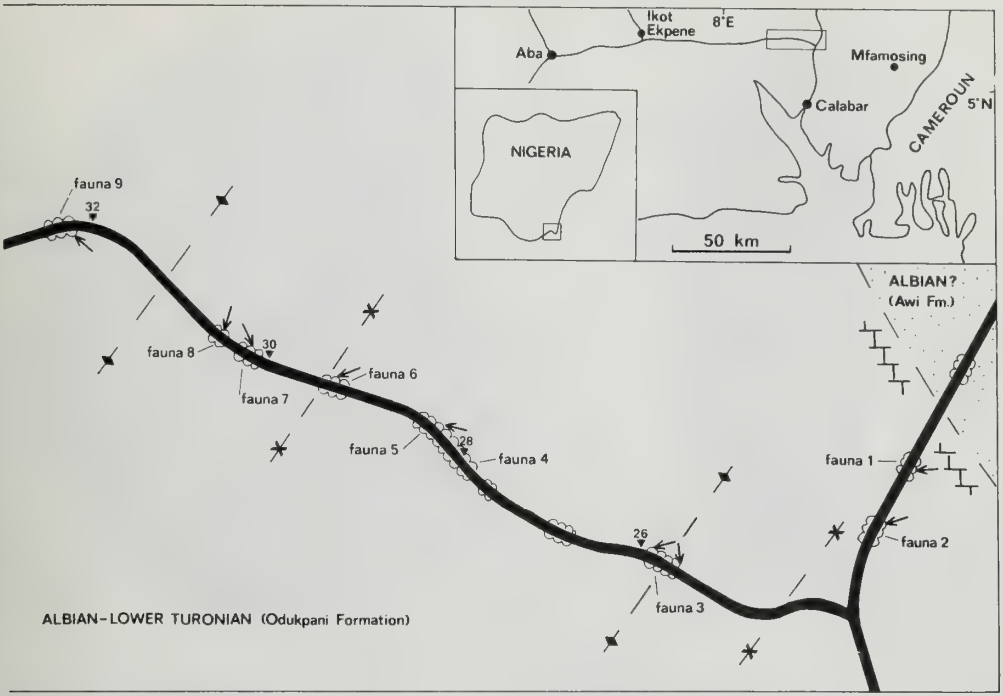

Ikot Ekpene
8°E
Aba
Mfamosing
Calabar
CAMEROUN
5°N
NIGERIA
50 km
ALBIAN?
(Awi Fm.)
fauna 9
32
fauna 8
30
fauna 7
fauna 6
fauna 5
28
fauna 4
fauna 1
fauna 2
26
fauna 3
ALBIAN–LOWER TURONIAN (Odukpani Formation)

Fig. 2 Map showing road section north of Calabar and localities of fossils mentioned in the text: eastern portion.

Systematic descriptions

Repositories. Register numbers prefixed by the abbreviation UIN are of specimens in the Department of Geology, University of Ilorin, Nigeria. Those prefixed by the letter C. are of specimens in the Department of Palaeontology, British Museum (Natural History), London.

Terminology. The following abbreviations are used. Dimensions (in mm): D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Whorl breadth and height are given for intercostal sections only. Figures in parentheses are dimensions as a percentage of the total diameter. Sutures: the terminology of Wedekind (1916), as revised by Wiedmann & Kullman (1981), is used. E, external lobe; L, lateral lobe; U, umbilical lobe; I, internal lobe. The terms 'inner' and 'outer ventrolateral tubercles' are used respectively for the *Treatise* (Arkell *et al.* 1957) terms 'lower' and 'upper ventrolateral tubercles'.

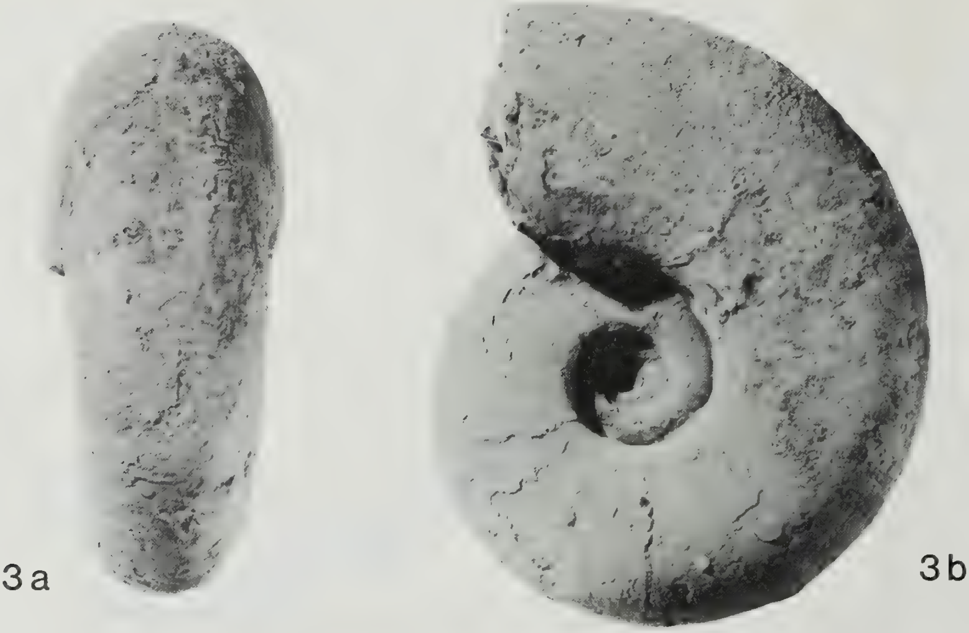
Localities. Unless otherwise stated, the material described is from cuttings on the Calabar–Ikot Ekpene road, south-east Nigeria. Certain specimens cannot be assigned with certainty to an exact horizon. Those that can are localized according to their distances from Calabar using the mileposts as reference points.

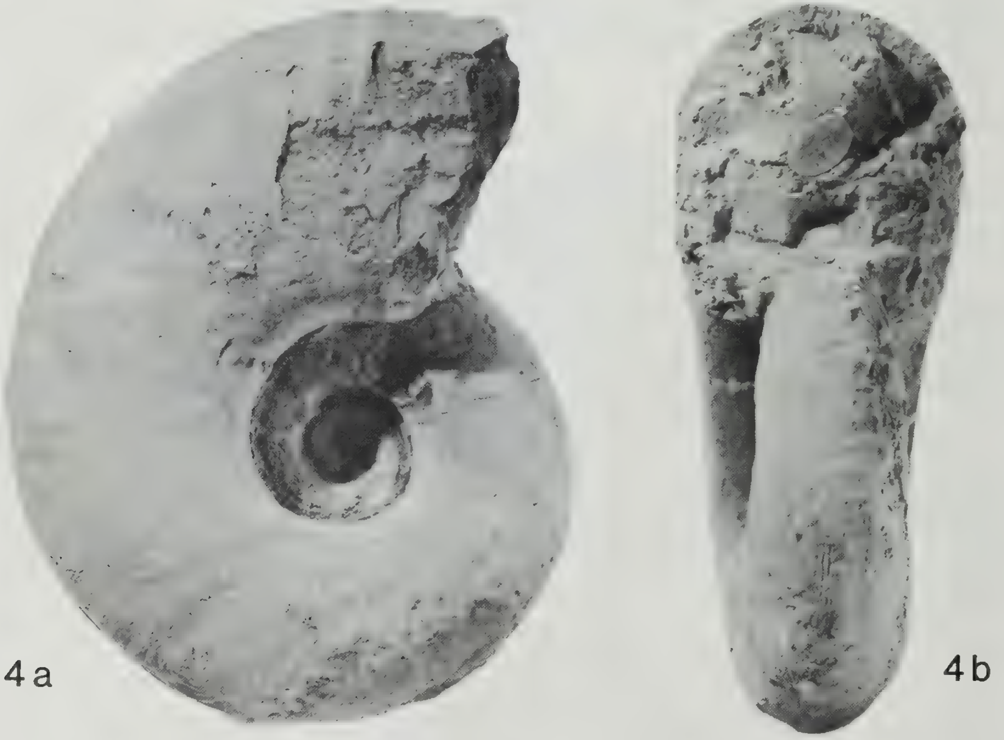
Superfamily **TETRAGONITACEA** Hyatt, 1900

Family **GAUDRYCERATIDAE** Spath, 1927

Genus ***ANAGAUDRYCERAS*** Shimizu, 1934

Type species. *Ammonites sacya* Forbes, 1846; by the original designation of Shimizu, 1934 (= *Ammonites buddha* Forbes, 1846, subj. syn.).





Figs 3, 4 *Anagaudryceras involvulum* (Stoliczka). Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar. Figs 3a, b, C.83113, ×1. Figs 4a, b, C.83478, ×1.

Anagaudryceras involvulum (Stoliczka, 1865)

Figs 3–4

1865 *Ammonites involvulus* Stoliczka: 150; pl. 75, figs 1a, 1b.
1865 *Ammonites sacya* Forbes; Stoliczka: 154; pl. 76, fig. 3 (only).
1895 *Lytoceras* (*Gaudryceras*) *involvulus* (Stoliczka) Kossmat: 32.
1935 *Gaudryceras* (*Anagaudryceras*) *utaturense* Shimizu: 176.
1956 *Anagaudryceras involvulum* (Stoliczka) Collignon: 68.
1966 *Anagaudryceras involvulum* (Stoliczka); Howarth: 219; pl. 1, figs 1, 2.
1975 *Anagaudryceras involvulum* (Stoliczka); Kennedy & Juignet: 77, fig. 1.
1976 *Anagaudryceras involvulum* (Stoliczka); Juignet & Kennedy: 49; pl. 1, figs 1a–c, 2a–c.

Material and occurrence. Three specimens (C.83113, C.83478, UIN 484.1) from the Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar.

Dimensions.	D	Wb	Wh	U
C.83113	90	36 (40)	39 (43·3)	26 (29)
C.83478	100	39 (39)	45 (45)	30 (30)
UIN 484.1	81	–	35 (43·2)	23 (28·4)

Description. These three fully septate specimens are evolute and moderately compressed, with the whorl sides rather flattened dorsally but converging ventrally to the broadly rounded venter. The whorls are a little higher than broad, at least at the largest preserved diameters. The umbilicus is moderately depressed, being a little less than one-third of the diameter in width. The umbilical shoulders are sharply rounded.

The shell in C.83113 is covered with very fine, dense, biconcave lirae which are coarsened at closely-spaced though irregular intervals. Where the shell is missing there are shallow, narrow constrictions taking the same path as the lirae. There are six constrictions on the last-preserved whorl but some are pronounced only on the ventral part of the whorl sides. They may be associated with very low, faint rib-like structures on the shell. In C.83478 and UIN 484.1 periodic deep constrictions associated with strong ribs appear at diameters in excess of 70–90 mm, and between these there are finer, more closely spaced ribs confined to the ventral half to two-thirds of the whorl sides.

The suture contains three saddles outside the umbilical shoulder. These are basically bifid with the two arms bifid again. In C.83113 L is deep and asymmetrically trifid but in C.83478 and UIN 484.1 it is shallower and less obviously trifid. There is a further small saddle between the umbilical shoulder and the umbilical seam but the internal suture is not displayed.

Remarks. In recent discussions of *Anagaudryceras*, Howarth (1965: 357–358) and Kennedy & Klinger (1979: 144–146) divided the genus into two groups. The group of *A. buddha* (Forbes 1846: 112; pl. 14, fig. 9), a probable synonym of *A. sacya* (Forbes 1846: 113; pl. 14, fig. 10), includes forms developing strong fold-like ribs in the adult stages. The group of *A. involvulum* (Stoliczka 1865: 150; pl. 75, fig. 1; pl. 76, fig. 3) includes weakly ornamented species which may still develop periodic ribbing in the later stages; the present material falls into the second group. It is closest to the main Cenomanian species *A. involvulum*, which, although slightly more evolute, has a similar gross morphology and ornamentation, developing deeper constrictions and periodic ribbing towards adulthood (see Stoliczka 1865: pl. 76, fig. 3). As Howarth (1965: 358) has pointed out, a major problem in the subdivision of this genus is the lack of reliable information concerning intraspecific variation. Apart from the present material only a handful of specimens from the Cenomanian of southern India (Stoliczka 1865), the Middle Cenomanian of north-west France (Kennedy & Juignet 1975, Juignet & Kennedy 1976) and the mid-Turonian of Angola (Howarth 1966) have been referred to *A. involvulum.* The main variation between these specimens is in ornamental strength: some are weakly ribbed (Stoliczka 1865: pl. 76, fig. 3; Kennedy & Juignet 1975; Juignet & Kennedy 1976: pl. 1, figs 1a–c, 2a–c; C.83113, Fig. 3a, b herein); others develop rather prominent ribbing in the later stages (Howarth 1966: pl. 1, figs 1, 2; UIN 484.1, C.83478, Fig. 4a, b herein).

A number of specific names are in use for post-Cenomanian members of the long-lived and conservative *A. involvulum* group (see list in Kennedy & Klinger, 1979: 146). Of these the Santonian *A. yamashitai* (Yabe 1903: 38; Matsumoto 1959: 138; pl. 37, figs 1a–d) is very like the Nigerian material. The Campanian–Maastrichtian *A. mikobokense* Collignon (1956: 59; pl. 8, fig. 1; Matsumoto 1959: 139; pl. 38, fig. 1; Howarth 1965: 358; pl. 4, figs 1–3) and *A. politissimum* (Kossmat 1895: 128; pl. 15, fig. 7; Collignon 1956: pl. 8, fig. 2) are also close but are distinctly more evolute, the latter being in addition more highly compressed.

Genus ***GAUDRYCERAS*** Grossouvre, 1894

Type species. *Ammonites mitis* Hauer, 1866; by the subsequent designation of Boule, Lemoine & Thévenin, 1906.

Gaudryceras beantalyense Collignon, 1956
Figs 5–6

1956 *Gaudryceras beantalyense* Collignon: 53; pl. 5, figs 1–3.
1965*a* *Gaudryceras beantalyense* Collignon; Collignon: 2; pl. 414, figs 1713, 1714.

Material and occurrence. Nine specimens (C.82155–6, C.83203–4, C.83209, C.83508–10, UIN 439.1) from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar.

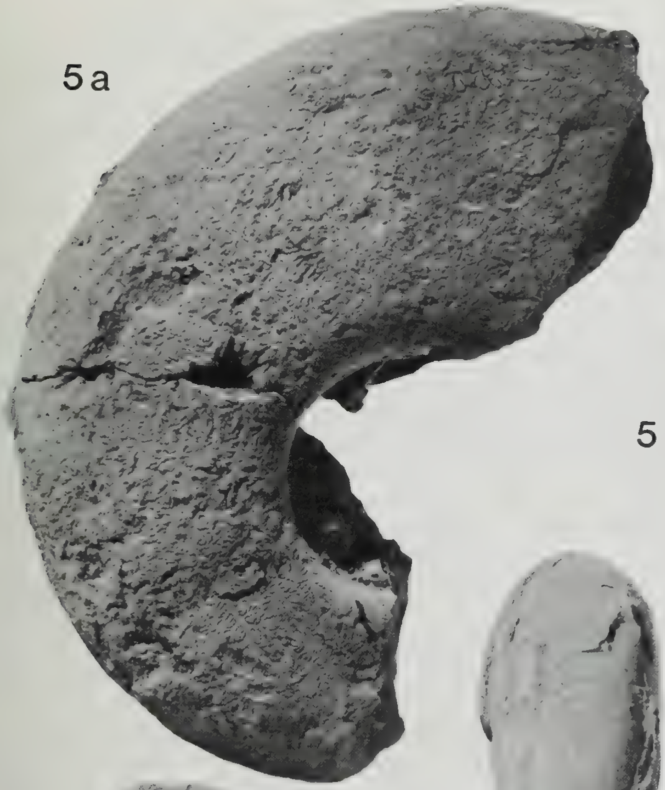
Dimensions.	D	Wb	Wh	U
C.83203	115	42·5 (37)	53 (46)	35 (30·5)
C.83510	70	26 (37)	30 (43)	29 (41·4)

Description. In the earliest stages the whorls are depressed, being markedly broader than high. At a diameter of about 35 mm whorl breadth and whorl height are approximately equal. Thereafter the whorls become moderately compressed, higher than broad, with rather flattened flanks and a broadly rounded venter. The phragmocone reaches a diameter in excess of 150 mm. In the early stages the shell is highly evolute but at a diameter of about 40–45 mm the whorls become embracing and the shell increasingly involute. It is covered with dense, very fine ribs which are almost invisible to the naked eye. There are rather deep constrictions on internal moulds in the early stages, four being present on the last preserved half whorl in C.83510. In the later stages the constrictions become fainter and more widely spaced. At no stage do they seem to be associated with strengthened ribs, ornamental style remaining constant during ontogeny. Towards adulthood a septal lobe may develop.

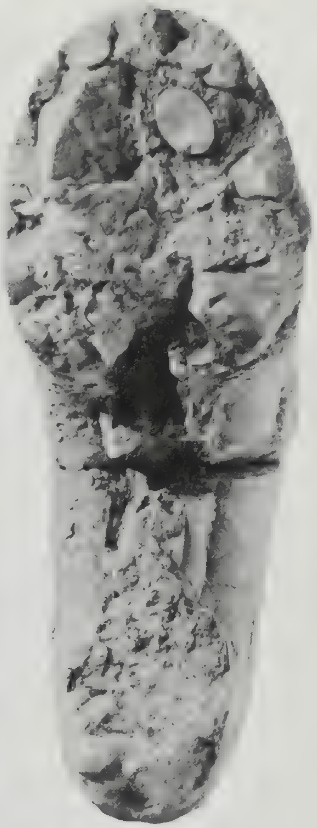
Remarks. Although a multitude of specific names have been proposed, three important groups can be distinguished within the genus *Gaudryceras* (see Howarth 1965: 360–362; Henderson 1970: 15–16; Kennedy & Klinger 1979: 128–129). The groups of *G. densiplicatum* (Jimbo 1894: 182; pl. 23, figs 1a, 1b) and *G. tenuiliratum* (Yabe 1903: 19; pl. 3, figs 3, 4) both include forms developing coarsely ribbed outer whorls. The third group, typified by *G. mite* (Hauer 1866: 305; pl. 2, figs 3, 4) and *G. varagurense* (Kossmat 1895: 122; pl. 17, fig. 5; pl. 18, figs 2a–c), includes forms retaining fine ribbing throughout ontogeny. The present specimens belong in the last group but are peculiar in the extreme fineness of their ribbing and the lack of periodic strengthened ribs. In these respects, and also in gross morphology, they cannot be distinguished from the Malagasy species *G. beantalyense* Collignon (1956: 53; pl. 5, figs 1–3; 1965*a*: 2; pl. 414, figs 1713, 1714), although this is of Coniacian age. *G.*

Figs 5, 6 *Gaudryceras beantalyense* Collignon. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. Figs 5a, b, C.83203, ×1. Figs 6a, b, C.83510, ×1.

Fig. 7 *Turrilites (Turrilites) scheuchzerianus* Bosc. Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar. C.82116, ×1; note interruptions in ribs on lower half of whorl sides. See also Fig. 8.



5a



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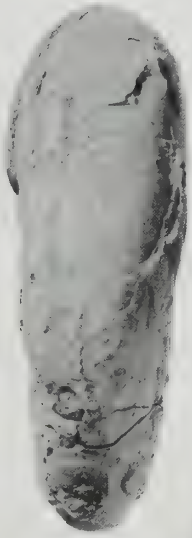
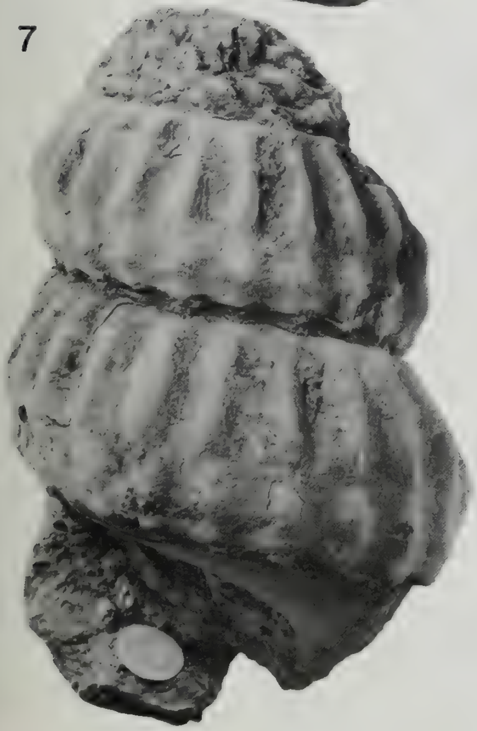


6a



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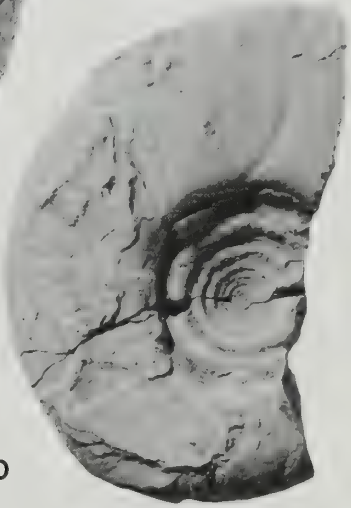


6b

analabense Collignon (1956: 54; pl. 6, figs 1–3; 1965*a*: 4; pl. 415, figs 1717, 1718), a contemporaneous form, is very close to *G. beantalyense* and may be a synonym.

Internal moulds of the outer whorls of the present material were previously misidentified (Zaborski 1982: 306, 323) as *Neodesmoceras* sp., which they closely resemble (compare, for example, Matsumoto & Saito 1954: 88; pl. 9, figs 1a–c; pl. 10, figs 1a–c; pl. 11, figs 1, 2). The discovery of the inner whorls, however, confirms the present identification.

Gaudryceras varicostatum van Hoepen, 1921

1921 *Gaudryceras varicostatum* van Hoepen: 7; pl. 2, figs 10–12; text-figs 3, 4.
1922 *Gaudryceras cinctum* (Crick ms) Spath: 118; pl. 9, figs 3a, 3b.
1979 *Gaudryceras varicostatum* van Hoepen; Kennedy & Klinger: 133; pl. 3, figs 1–3; pl. 4; pl. 7, fig. 2; pl. 14, fig. 11; text-fig. 1 (with synonymy).

MATERIAL AND OCCURRENCE. Three specimens (C.83141–3) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

REMARKS. These three fragmentary specimens, members of the *Gaudryceras mite* group, are all crushed and not worth figuring. On the later massive whorls their ornament consists of relatively strong, equally developed, sharp, biconcave lirae identical to that in *G. varicostatum* van Hoepen (1921: 7; pl. 2, figs 10–12; text-figs 3, 4), a species discussed in detail by Kennedy & Klinger (1979: 133). *G. varicostatum* is known from the Coniacian–Campanian of South Africa and the Malagasy Republic. The Campanian–Maastrichtian *G. propemite* Marshall from New Zealand (see Henderson 1970: 15; pl. 2, fig. 1) may be a synonym.

Superfamily **TURRILITACEAE** Meek, 1876

Family **TURRILITIDAE** Meek, 1876

Subfamily **TURRILITINAE** Gill, 1871

Genus ***TURRILITES*** Lamarck, 1801

Subgenus ***TURRILITES*** Lamarck, 1801

TYPE SPECIES. *Turrilites costata* Lamarck, 1801; by original designation.

Turrilites (Turrilites) scheuchzerianus Bosc, 1802

Figs 7, 8

1802 *Turrilites Scheuzeriana* Bosc: 190.
1925 *Turrilites scheuchzerianus* Bosc; Diener: 84 (with synonymy).
1955 *Turrilites* (*Euturrilites*) *scheuchzerianus* Bosc; Reyment: 13; pl. 1, fig. 2.
1966 *Euturrilites scheuchzerianus* Bosc emend. Sharpe; Collignon: 24; pl. 12, fig. 1 (with synonymy).

MATERIAL AND OCCURRENCE. Fifteen specimens (C.82115–8, C.82124, C.82150, C.83093, C.85254, UIN 471.1–7) from the Odukpani Formation (Middle Cenomanian). UIN 471.1–471.7, C.83093 and C.85254 are from a horizon exposed 27·9 km from Calabar; the remainder, although not precisely localized, are almost certainly from the same level.

REMARKS. This well-known species is represented by variable material. The ribs often tend to be interrupted in the early whorls but are usually entire and slightly curved in the later stages. There are, however, a few individuals which at adulthood show one or two interruptions in the ribs on the lower half of the whorls, these specimens thus being intermediate between *T. scheuchzerianus* and *T. costatus* Lamarck: see below.

Turrilites (Turrilites) costatus Lamarck, 1801

Figs 9, 10

1801 *Turrilites costata* Lamarck: 102.
1925 *Turrilites costatus* Lamarck; Diener: 81 (with synonymy).
1957 *Turrilites* (*Turrilites*) *costatus* Lamarck; Reyment: 56; pl. 9, fig. 3.

1962 *Turrilites costatus* Lamarck; Wiedmann: 192 (with synonymy).
1971 *Turrilites* (*Turrilites*) *costatus* Lamarck; Kennedy: 30; pl. 6, fig. 3; pl. 8, figs 12, 14.
1976 *Turrilites* (*Turrilites*) *costatus* Lamarck; Juignet & Kennedy: 63; pl. 3, figs 16, 18, 19 (with synonymy).

MATERIAL AND OCCURRENCE. Twenty-four specimens (C.83103–4, C.83467–71, C.85252–3, UIN 421.1–15) from the Odukpani Formation (Middle Cenomanian). C.85252 and C.85253 are from a horizon exposed at 27·9 km from Calabar, the remainder at 28·3 km from Calabar.

REMARKS. This species occurs at two horizons. The specimens (C.85252, C.85253) found at 27·9 km from Calabar accompany the material referred above to *Turrilites scheuchzerianus*, which, as mentioned, includes *T. costatus*-like variants. In these two individuals, rib subdivision is pronounced and they must be referred to *T. costatus*. The second and larger population occurs slightly higher, at 28·3 km from Calabar. Its members are morphologically highly variable, rib development on the upper whorl sides being markedly inconsistent. The population is, in fact, almost exactly intermediate in mean structure between *T. costatus* and *T. acutus* Passy. Some variants show the long ribs typical of the former species, others are like *T. acutus* in showing more rudimentary ribs.

***Turrilites* (*Turrilites*) *acutus* Passy, 1832**

1832 *Turrilites acutus* Passy: 334; Atlas p. 7; pl. 16, figs 3, 4.
1925 *Turrilites acutus* Passy; Diener: 79 (with synonymy).
1965 *Turrilites* (*Turrilites*) *acutus* Passy; Clark: 54; pl. 19, fig. 7 (with synonymy).
1971 *Turrilites* (*Turrilites*) *acutus* Passy; Kennedy: 30; pl. 7, figs 7, 8.
1976 *Turrilites* (*Turrilites*) *acutus* Passy; Juignet & Kennedy: 65; pl. 3, fig. 6; pl. 4, figs 1–3 (with synonymy).

MATERIAL AND OCCURRENCE. A single specimen (C.83114) from the Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar.

REMARKS. This familiar species, discussed by Kennedy (1971: 30) and Juignet & Kennedy (1976: 65), is represented by a sole specimen from a horizon exposed 30·3 km from Calabar, marking the highest known occurrence of *Turrilites* in Nigeria. As mentioned above, individuals transitional between *T. costatus* and *T. acutus* occur lower in the Odukpani Formation. Successively younger populations, therefore, show a progressive reduction in rib development on the upper whorl sides.

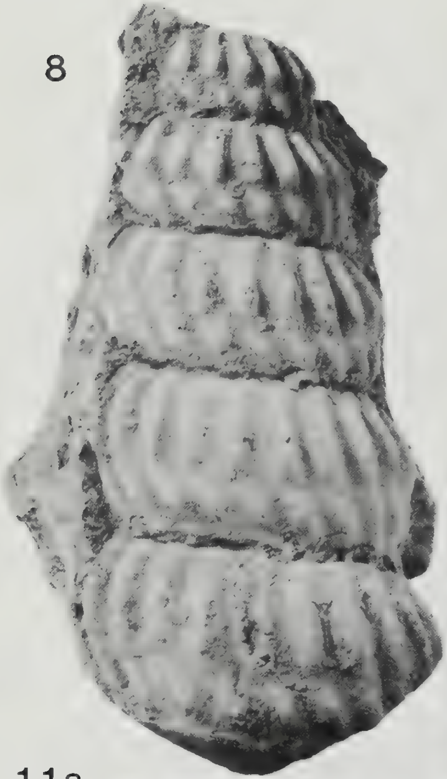
Subfamily **NOSTOCERATINAE** Hyatt, 1894

Genus ***PSEUDOXYBELOCERAS*** Wright & Matsumoto, 1954

Subgenus ***PARASOLENOCERAS*** Collignon, 1969

TYPE SPECIES. *Parasolenoceras splendens* Collignon, 1969; by original designation.

REMARKS. Collignon (1969: 44) proposed the genus *Parasolenoceras* for specimens from the Lower Campanian of the Malagasy Republic showing a mode of coiling and ornament similar to that in *Solenoceras* Conrad, but which differ in the separation of the shafts of the shell. Subsequently Ward & Mallory (1977) introduced the subgenus *Pseudoxybeloceras* (*Cyphoceras*) (type species *Ancyloceras*? *lineatus* Gabb) for forms having a very similar coiling and ornamentation. *P.* (*Cyphoceras*) was defined by its relatively large shell coiled in a single plane, its ovoid whorl section, the presence of a single row of tubercles either side of the venter, and the separation of the shafts of the shell. Morphologically *P.* (*Cyphoceras*) is therefore intermediate between *P.* (*Pseudoxybeloceras*) Wright & Matsumoto and *Solenoceras*; Ward & Mallory (1977) considered it to be a subgenus of the former. In all respects *P.* (*Cyphoceras*) conforms with *Parasolenoceras*; Ward & Mallory (1977: 611) themselves considered the probability that its type species, *Parasolenoceras splendens* Collignon (1969: 44; pl. 530, figs 2087, 2088), belongs to *P.* (*Cyphoceras*). As the name *Parasolenoceras* has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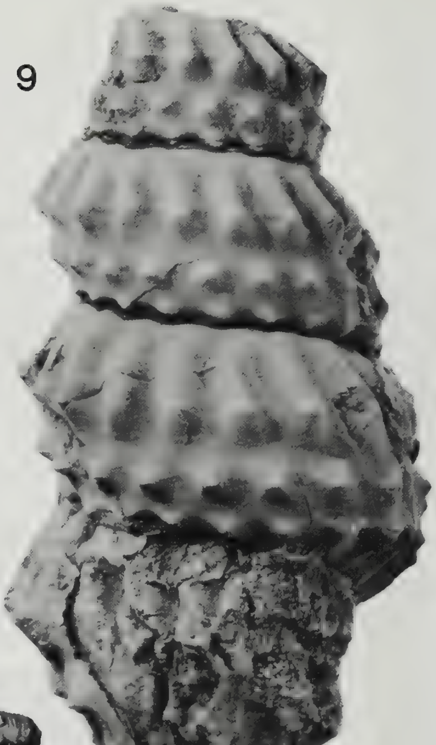
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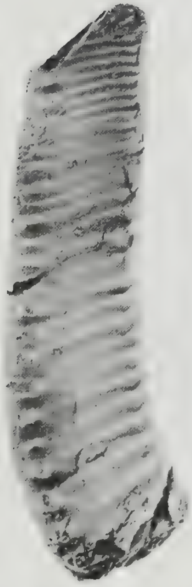
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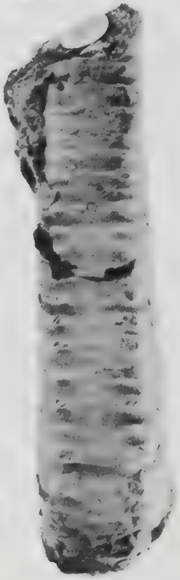
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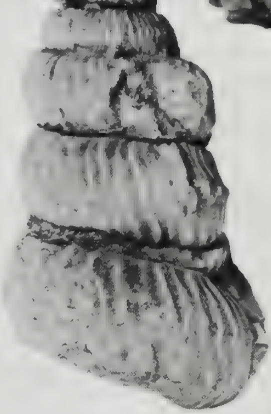
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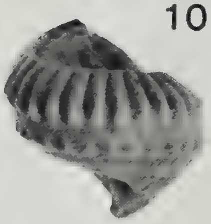
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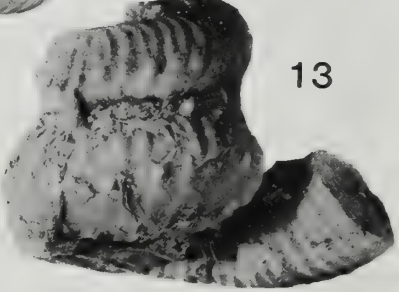
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priority over *P.* (*Cyphoceras*), the latter name should be suppressed in its favour. The genus *Christophoceras* Collignon (1969: 47) differing from *Parasolenoceras* only in the periodic development of large inner ventrolateral tubercles, this too is here regarded as a synonym. As suggested by Ward & Mallory (1977), *Parasolenoceras* is probably best treated as a subgenus of *Pseudoxybeloceras*.

At present the following species can be referred to *Pseudoxybeloceras* (*Parasolenoceras*): *Ancyloceras*? *lineatus* Gabb 1869 (see Matsumoto 1959: 162; pl. 40, figs 1a–d; pl. 41, figs 1a–c; Ward & Mallory 1977: 613; pl. 1, figs 1–7) and *Pseudoxybeloceras* (*Cyphoceras*) *nanaimoense* Ward & Mallory (1977: 615; pl. 2, figs 1–3; pl. 3, figs 1–3; text-fig. 3) from the Pacific Coast of North America; *Parasolenoceras splendens* Collignon (1969: 44; pl. 530, figs 2087, 2088) and *Christophoceras ramboulei* Collignon (1969: 47; pl. 531, fig. 2093) from the Malagasy Republic; *Pseudoxybeloceras bicostatum* Henderson (1970: 31; pl. 4, fig. 2) and *P. compressum* Henderson (1970: 31; pl. 4, fig. 4) from New Zealand; and an undescribed species from the Coniacian–Santonian of Hokkaido mentioned by Ward & Mallory (1977: 617). In addition *Hamites*(?) *clinensis* Adkins (1929: 208; pl. 6, figs 10, 11) from the Taylor Formation of Texas, dated by Young (1963) as Lower Campanian, may belong here.

The majority of previously-described species are of Campanian age though Henderson (1970: 31–32) reported *P.* (*Parasolenoceras*) *bicostatum* as having a possible range from Santonian to Maastrichtian. According to Ward & Mallory (1977), *P.* (*Parasolenoceras*) appeared in Coniacian or early Santonian times and gave rise to *Solenoceras* in the late Campanian. The fragment described below conforms well in all observable respects with *P.* (*Parasolenoceras*) but is of Upper Campanian age, making it amongst the youngest representatives of the subgenus. Typical diminutive *Solenoceras* occurs higher in Nigeria, being present in Lower Maastrichtian beds containing *Pachydiscus dossantosi* (Maury) and *Sphenodiscus* sp. at Akanu, some 90 km north-west of Calabar.

Pseudoxybeloceras (Parasolenoceras) aff. ***splendens*** Collignon, 1969

Fig. 11a, b

Compare: 1969 *Parasolenoceras splendens* Collignon: 44; pl. 530, figs 2087, 2088.

MATERIAL AND OCCURRENCE. A single specimen (C.83155) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

DESCRIPTION. The material consists of a single fragment of what appears to be the distal part of the penultimate shaft of the shell. The last two shafts were not in contact. The whorl section is ovoid with the venter somewhat flattened. There are fairly dense ribs at the adapical end of the specimen, becoming coarser and more distant adorally. In most cases each rib bears a pair of tubercles, one each side of the venter, though occasionally one is absent or weakly developed. The tubercles become more prominent adorally. The ribs are indistinct between the tubercles, and along the dorsum where they are obvious only either side of two constrictions, one at the adoral end of the specimen and the other, shallower, 35 mm adapical of the first.

The suture is not displayed.

Fig. 8 *Turrilites (Turrilites) scheuchzerianus* Bosc. Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar. C.82117, ×1; note interruptions in ribs on lower half of whorl sides. See also Fig. 7.

Figs 9, 10 *Turrilites (Turrilites) costatus* Lamarck. Odukpani Formation (Middle Cenomanian), 28·3 km from Calabar. Fig. 9, C.83467, ×1. Fig. 10, C.83470, ×1.

Fig. 11a, b *Pseudoxybeloceras (Parasolenoceras)* aff. *splendens* Collignon. Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83155, ×1.

Figs 12, 13 *Didymoceras* aff. *hornbyense* (Whiteaves). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. Fig. 12, C.85263, ×1. Fig. 13, C.85264, ×1. These spires probably represent the early whorls of specimens such as that shown in Fig. 14.

Remarks. This specimen is less compressed than *Pseudoxybeloceras* (*Parasolenoceras*) *lineatum* (Gabb) (see Matsumoto 1959: 162; pl. 40, figs 1a–d; pl. 41, figs 1a–c; Ward & Mallory 1977: 613; pl. 1, figs 1–7) and much less so than *P.* (*Parasolenoceras*) *compressum* Henderson (1970: 31; pl. 4, fig. 4). The former species also shows occasional duplication of the tubercles. *P.* (*Parasolenoceras*) *bicostatum* Henderson (1970: 31; pl. 4, fig. 2) is smaller and with denser ribbing. *P.* (*Parasolenoceras*) *ramboulei* (Collignon 1969: 47) is quite different, showing periodic strengthened ribs with prominent inner and outer tubercle rows. *P.* (*Parasolenoceras*) *nanaimoense* (Ward & Mallory 1977: 615; pl. 2, figs 1–3; pl. 3, figs 1–3; text-fig. 3) shows periodic strong spines associated with two or three ribs. *P.* (*Parasolenoceras*)? *clinensis* (Adkins 1929: 208; pl. 6, figs 10, 11) has a less regular tubercle development, each being normally associated with a pair of ribs. This leaves *P.* (*Parasolenoceras*) *splendens* Collignon (1969: 44; pl. 530, figs 2087, 2088) as closest to the present material in shape and ornament, although it is of a somewhat older, Lower Campanian, age.

Genus ***DIDYMOCERAS*** Hyatt, 1894

Type species. *Ancyloceras*? *nebrascense* Meek & Hayden, 1856; by the original designation of Hyatt, 1894.

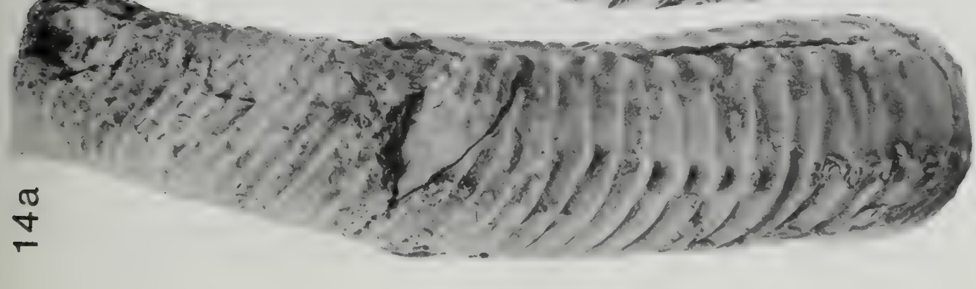
Remarks. *Didymoceras* and related genera were discussed at length by Howarth (1965: 371–374). He concluded that *Cirroceras* Conrad is an unusable generic name which should be abandoned in favour of *Didymoceras* Hyatt, of which *Bostrychoceras* Hyatt was considered a synonym. *Nostoceras* Hyatt was retained as a relatively closely-defined genus. Although these conclusions were largely accepted by Matsumoto (1967: 339–341) and Lewy (1969: 110–111), the highly variable and intergradational nature of these heteromorph genera has led to a rather flexible treatment by authors. Klinger (1976: 63–64) placed all the above in the 'genus-group' *Didymoceras*. Although Jones (1963: 20) and Klinger (1976: 63–64) have pointed out that the distinction between *Nostoceras* and *Didymoceras* may well be entirely artificial, the two genera are separated here, following Howarth (1965). *Didymoceras* is therefore distinguished by its characteristically larger size, typically loosely coiled spire with the retroversal hook breaking away gradually, and its more complex ribbing with variably-developed tuberculation.

Didymoceras aff. ***hornbyense*** (Whiteaves, 1895)
Figs 12–14

Compare: 1895 *Heteroceras hornbyense* Whiteaves: 316.
1903 *Heteroceras hornbyense* Whiteaves; Whiteaves: 332; pl. 42, figs 1–4.
1903 *Anisoceras cooperi* (Gabb); Whiteaves: 336; pl. 43, fig. 1.
1952 *Nostoceras hornbyense* (Whiteaves) Usher: 103; pl. 27, figs 1, 2; pl. 31, fig. 23.
1952 *Anisoceras cooperi* (Gabb); Usher: 107; pl. 29, fig. 1.
1958 *Didymoceras whiteavesi* Anderson: 196.
1963 *Didymoceras* aff. *D. hornbyense* (Whiteaves) Jones: 30; pl. 23, fig. 1.

Material and occurrence. Six specimens (C.83144–5, C.83147–8, C.83152, UIN 499.1) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar. In addition four other specimens (C.83146, C.83504, C.85263–4) from the same locality probably belong here.

Description. The specimens reach a large size. The whorls are more or less circular in cross section, with a diameter of about 30–40 mm at the retroversal point of the hook. Only the adoral part of the spire is known with certainty; here it appears to be loosely coiled with the retroversal hook breaking away gradually. The hook itself may be sharply retroversal with the two limbs almost in contact at the level of the aperture. The sutures are seen only in C.83147, in which the phragmocone includes the whole of the proximal limb of the retroversal hook.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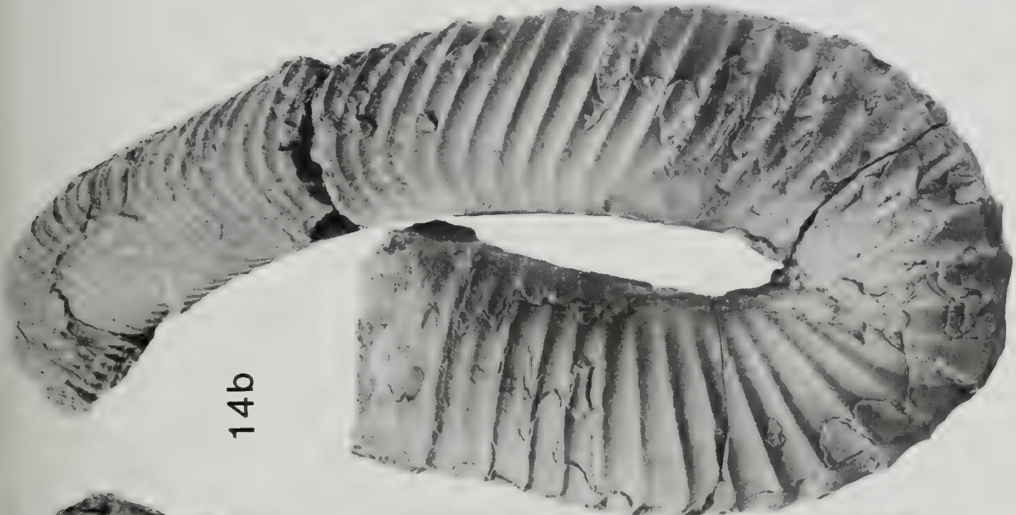
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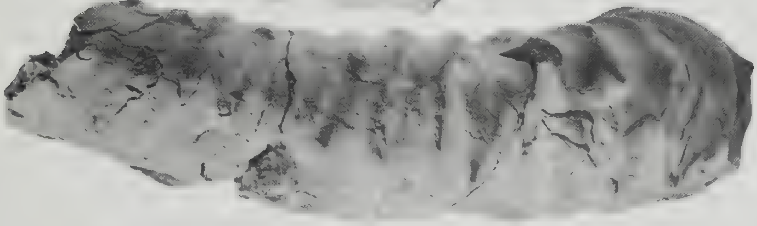
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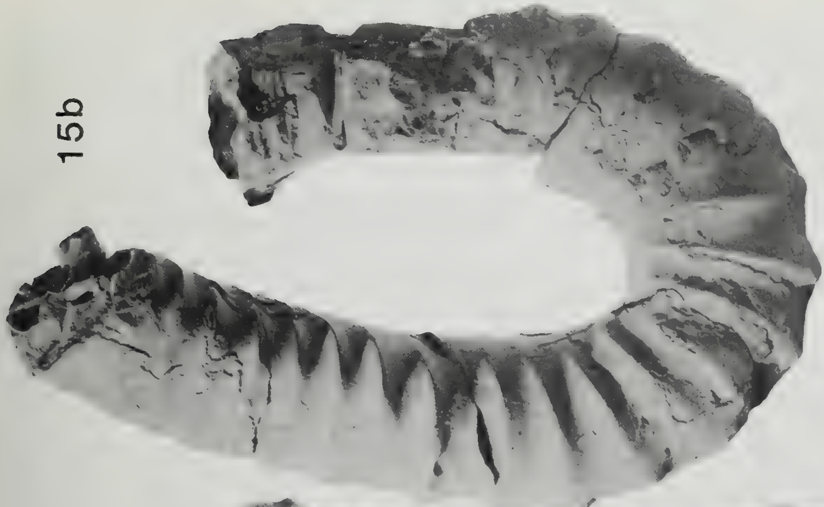
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Fig. 14a, b *Didymoceras* aff. *hornbyense* (Whiteaves). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83144, ×0·75. See also Figs 12, 13.

Fig. 15a, b *Didymoceras* aff. *cheyennense* (Meek & Hayden). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83503, ×0·75.

The last part of the spire and the early part of the retroversal hook bear fine, sporadically tuberculated ribs with an eccentric course. On the proximal limb of the hook the ribs become stronger, sharper and more distant: they die out along the dorsum. Typically, along the venter each rib bears a pair of weak to moderately well developed tubercles. The tubercles, at first on the lower surface of the whorl at the adoral end of the spire, gradually pass onto the periphery of the retroversal hook. Some ribs lack tubercles, occasionally some bifurcate, and in places some ribs zigzag between opposite and successive tubercles. On the distal limb of the hook each rib consistently carries a pair of tubercles though they lose a little strength adorally. At this stage the ribs show no tendency to zigzag between the tubercles. On the proximal limb of the hook the ribs are prorsiradiate, on the first part of the distal limb they are rursiradiate, and finally they become rectiradiate. The interspaces are wider than the ribs. The aperture is collared.

Occurring with these retroversal hooks are a number of incomplete spires (C.83146, C.83504, C.85263–4; Figs 12, 13), which are high with tight dextral or sinistral coiling. Their early whorls bear fine, dense, sharp curved ribs which become somewhat coarser and more distant adorally. Tubercles are developed on the majority of the ribs in two rows, one close to the middle of the whorl and the other lower down, close to the line of contact with the succeeding whorl. Between the tubercles the ribs are subdued or absent. Although none of these spires was found attached to the retroversal hook, it seems probable that they represent the early whorls of the material described above. One of the spires (C.85264, Fig. 13) shows the last whorl clearly breaking away towards the apex of the spire.

REMARKS. Jones (1963: 30–31) has reviewed the confused nomenclature of the nostoceratid ammonites of the Pacific Coast of North America. Of the four proposed names *Ammonites*? *cooperi* Gabb 1864, *Hamites vancouverensis* Gabb 1864, *Heteroceras hornbyense* Whiteaves 1895 and *H. perversum* Whiteaves 1895, only *H. hornbyense* can be adequately diagnosed. The precise relationships between these forms are unclear but *H. hornbyense* and the excellent specimen figured by Whiteaves (1903: pl. 43, fig. 1) as *Anisoceras cooperi* (Gabb) (= *Didymoceras whiteavesi* Anderson 1958: 196) may well be conspecific. The present specimens find their closest relationships with these North American forms, agreeing well in size and ornamental style. The retroversal hook figured by Jones (1963: pl. 23, fig. 1) as *Didymoceras* aff. *hornbyense* is particularly close in size, ornament and mode of coiling. The general features of the tuberculation are similar and the typical zigzagging of the ribs between the two rows of tubercles is shown by both. In general, however, the North American forms tend to show a less consistent tubercle development. Each tubercle is often associated with more than one rib, or is developed only on every second or third rib. In addition, the spire in *D. hornbyense* is rather broad and flat (Whiteaves 1903: pl. 42, figs 1–4; Usher 1952: pl. 27, figs 1, 2), unlike those described above in which the last whorl of the spire seems to break away in an adapical direction. Although no complete specimen has been found and a definite reconstruction of an entire shell cannot yet be produced, it seems possible that the present material had a mode of coiling similar to that in *Nostoceras* (*Anaklinoceras*) Stephenson (1941: 414), with the retroversal hook positioned above the spire, but this does not necessarily indicate a close relationship between *N.* (*Anaklinoceras*) and the present material. As Lewy (1969: 109–110) points out, in these heteromorphs the plane of the body chamber may form a great variety of angles with the axis of coiling of the spire. In size and ornament *N.* (*Anaklinoceras*) clearly has its affinities with *N.* (*Nostoceras*) (see Stephenson 1941), while in these respects the present material is closer to *Didymoceras*. A spire from the basal Nkporo Shale in Nigeria described by Reyment (1955: 13; pl. 1, fig. 3) as *Didymoceras hornbyense* (Whiteaves) is similar to those described here and may be conspecific.

As noted by Jones (1963: 31), the three species *Nostoceras mexicanum* Anderson (1958: 196; pl. 58, fig. 3), *Didymoceras kernense* Anderson (1958: 196; pl. 65, figs 1, 1a, 2) and *Exiteloceras desertense* Anderson (1958: 202; pl. 66, figs 2, 2a) are all based on fragments and cannot be properly diagnosed. All show an ornament similar to that in *D. hornbyense* and appear to be related to it. *Didymoceras fresnoense* Anderson (1958: 197; pl. 68, fig. 2) and *Exiteloceras bennisoni* Anderson (1958: 210; pl. 72, fig. 7) also belong in *Didymoceras*, but their precise relationships are unclear.

Didymoceras aff. ***cheyennense*** (Meek & Hayden, 1856)

Fig. 15a, b

Compare: 1856 *Ancyloceras*? *Cheyennense* Meek & Hayden: 71.
1876 *Heteroceras*? *Cheyennense* (Meek & Hayden); Meek: 483; pl. 21, figs 2a, 2b (with synonymy).
1973 *Didymoceras cheyennense* (Meek & Hayden); Gill & Cobban: 10, text-fig. 5c.

MATERIAL AND OCCURRENCE. A single specimen (C.83503) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

DESCRIPTION. This large specimen consists only of the loosely coiled last part of the spire and the retroversal hook which breaks away gradually. The ornament consists of very coarse distant ribs each of which normally carries a pair of strong tubercles, although one or both may be absent especially on the proximal limb of the hook. The ribs sometimes bifurcate and may zigzag between the rows of tubercles, and there are a few intercalated ribs. The aperture is rather strongly collared.

REMARKS. In its coiling and general ornamental style the present specimen is essentially similar to the material described above as *Didymoceras* aff. *hornbyense*, differing mainly in its much coarser ornament. The two may represent varieties of a single species, although none of several unidentifiable heteromorph fragments also collected in the basal Nkporo Shale appears to be intermediate. For the present, therefore, this specimen is best compared with *Didymoceras cheyennense* (Meek & Hayden), a species proposed (Meek & Hayden 1856: 71) for a small fragment (see Meek 1876: pl. 21, figs 2a, 2b) and as such difficult to diagnose. Gill & Cobban (1973: text-fig. 5c), however, gave a restoration of a complete shell under this name. The holotype and this restoration agree with the Nigerian specimen in size and coarseness of the ribbing and the tuberculation on the retroversal hook. In *D. cheyennense*, however, each tubercle on the proximal limb of the retroversal hook is associated with two coarse ribs, while in the present specimen this part of the shell shows fine ribbing without tubercles.

Superfamily **DESMOCERATACEAE** Zittel, 1895

Family **DESMOCERATIDAE** Zittel, 1895

Subfamily **PUZOSIINAE** Spath, 1922

Genus ***PUZOSIA*** Bayle, 1878

Subgenus ***ANAPUZOSIA*** Matsumoto, 1954

TYPE SPECIES. *Puzosia buenaventura* Anderson, 1938; by the original designation of Matsumoto, 1954.

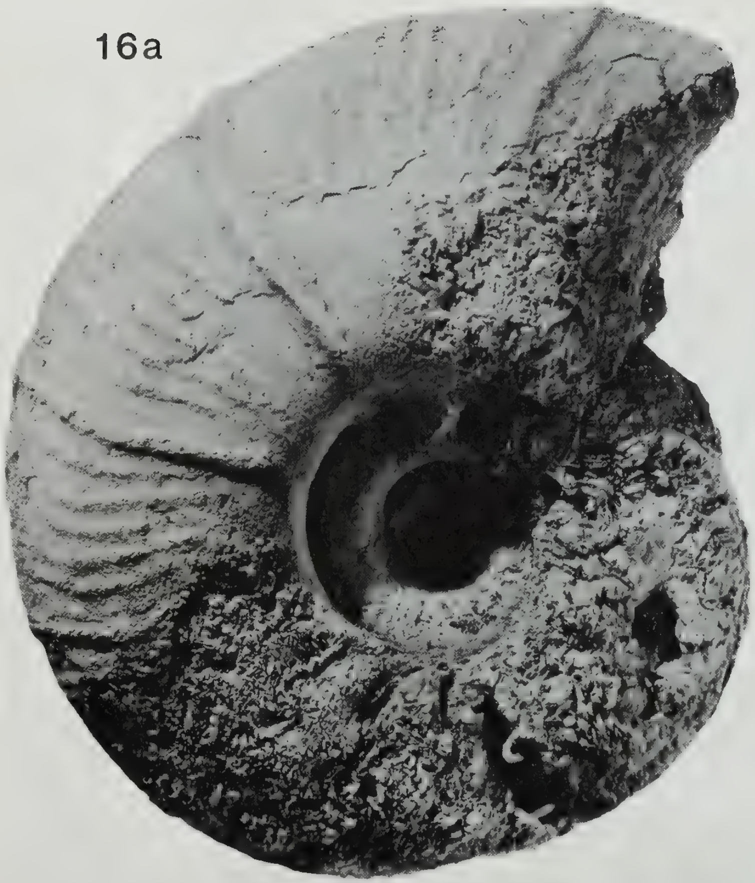
REMARKS. In *Puzosia* (*Anapuzosia*) the ribs appear at or near the umbilical margin, while in *P.* (*Puzosia*) Bayle they occur only on the ventral parts of the whorl sides. This subgenus is discussed by Matsumoto (1954), Renz (1972), Cooper (1978) and Wright & Kennedy (1981).

Puzosia (Anapuzosia) cf. ***dibleyi*** (Spath, 1922)

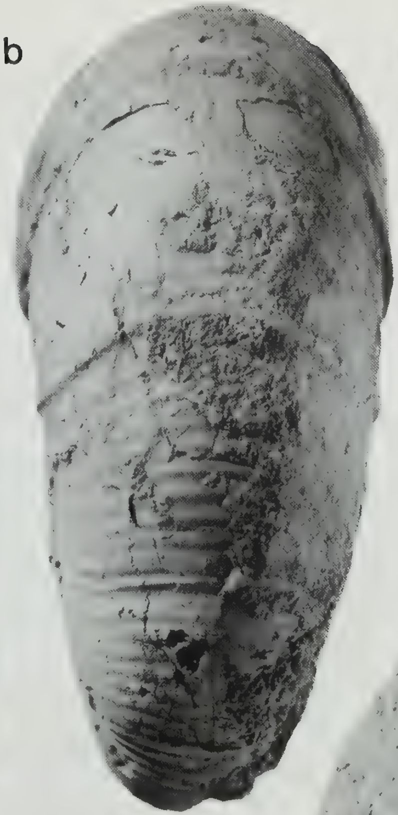
Fig. 16a, b

1855 *Ammonites austeni* Sharpe: 28; pl. 12, fig. 2 (only).
1922 *Austiniceras dibleyi* Spath: 127.
1931 *Puzosia matheroni* (d'Orbigny); Douvillé: 39; pl. 2, figs 5a, 5b (*non* d'Orbigny).
1951 *Austiniceras dibleyi* Spath; Wright & Wright: 19.

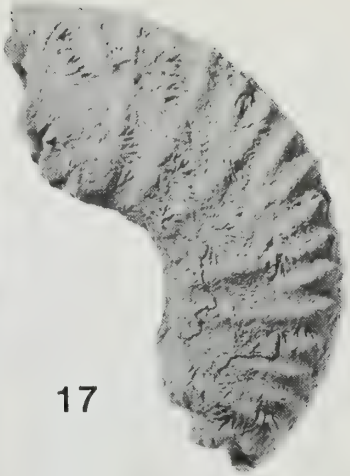
16a



16b



17



18

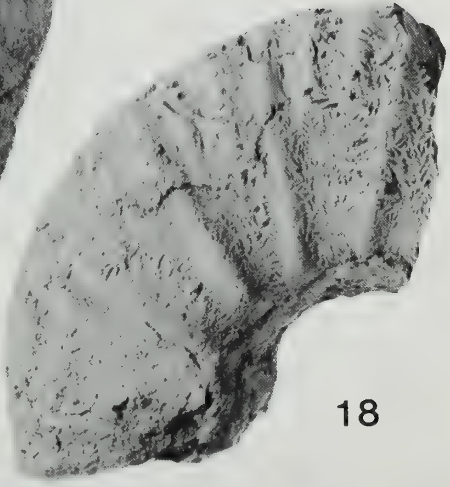


Fig. 16a, b *Puzosia (Anapuzosia)* cf. *dibleyi* (Spath). Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar. C.83119, ×1.
Figs 17, 18 *Pachydiscus (Pachydiscus) dossantosi* (Maury). Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. Fig. 17, C.83206, ×1. Fig. 18, C.83207, ×1. See also Fig. 20.

1971 *Austiniceras dibleyi* Spath; Kennedy: 39; pl. 13, figs 1, 2; pl. 14, fig. 4.
1978 *Puzosia* (*Anapuzosia*) *dibleyi* (Spath) Cooper: 78; figs 11A, 14B, 14C, 15B, 15C.
1981 *Puzosia* (*Anapuzosia*) *dibleyi* (Spath); Wright & Kennedy: 19; pl. 1, fig. 2; pl. 2, fig. 4.

MATERIAL AND OCCURRENCE. A single specimen (C.83119) from the Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar.

DESCRIPTION. The shell is moderately evolute, a little over half the previous whorl being covered. The whorls are moderately compressed with broadly rounded flanks converging upon the rounded venter. There are nine major sinuous ribs on the last preserved whorl originating at the umbilical shoulder. These ribs are associated with constrictions on the internal mould. Between the major ribs are five to nine intercalated, less pronounced ribs, some of which arise just outside the umbilical shoulder, others more ventrally on the flank.

REMARKS. This specimen agrees closely with *Puzosia* (*Anapuzosia*) *dibleyi* (Spath) in gross morphology and ornamentation. An Angolan individual figured by Kennedy (1971: pl. 13, fig. 1) is an almost exact match but is a little more compressed. The English Chalk material (Kennedy 1971: pl. 13, fig. 2; pl. 14, fig. 4; Wright & Kennedy 1981: pl. 1, fig. 2; pl. 2, fig. 2) is crushed, making comparison in this respect difficult. Hitherto *P.* (*A.*) *dibleyi* has been known only from southern England (see above) and Angola (Douvillé 1931, Cooper 1978) and in both places it characterizes beds of uppermost Cenomanian age. It is therefore typical of a higher horizon than the Nigerian specimen.

The Albian species *P.* (*Anapuzosia*) *multicostata* Renz (1972: 707; pl. 2, figs 1, 2; pl. 3, fig. 1; pl. 9, fig. 4), *P.* (*A.*) *saintoursi* Collignon (1963: pl. 263, fig. 1150; pl. 266, fig. 1157) and *P.* (*A.*) *colusaensis* (Anderson 1902: 96; pl. 5, figs 128, 129; pl. 10, fig. 200) all have more numerous, finer, denser intercalated ribs and typically show fewer major ribs.

Family **PACHYDISCIDAE** Spath, 1922

Genus ***PACHYDISCUS*** Zittel, 1884

Subgenus ***PACHYDISCUS*** Zittel, 1884

TYPE SPECIES. *Ammonites neubergicus* Hauer, 1858; by the subsequent designation of Grossouvre, 1894.

Pachydiscus (Pachydiscus) egertoni (Forbes, 1846)

Fig. 19a, b

1846 *Ammonites Egertoni* Forbes: 108; pl. 9, fig. 1.
1864 *Ammonites egertonianus* Forbes; Stoliczka: 104; pl. 53.
1898 *Pachydiscus egertonianus* (Forbes) Kossmat: 159; pl. 21, figs 4a–c.
? 1955 *Pachydiscus* aff. *stallauensis* Imkeller; Reyment: 17 (*non* Imkeller).
? 1957 *Pachydiscus* aff. *stallauensis* Imkeller; Reyment: 63; pl. 11, figs 2a, 2b (*non* Imkeller).
1959 *Pachydiscus egertoni* (Forbes); Matsumoto: 42, text-fig. 17.

MATERIAL AND OCCURRENCE. Two specimens (C.83140, C.83500) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83500	102	33 (32·2)	41 (40)	31 (30·4)
	72	24 (33·3)	31 (43)	20 (28)
	51	18 (35·3)	21 (41)	13 (25·8)

DESCRIPTION. The phragmocone reaches a diameter of at least 150 mm. The whorls are compressed, whorl height increasing a little more rapidly than whorl breadth during ontogeny, the flanks being flattened and the venter rounded. The shell is moderately evolute, a little over half the previous whorl being covered at the largest diameter seen (150 mm). The umbilicus widens slightly during ontogeny. The ornament consists of narrow rounded ribs which are pronounced just outside the umbilical shoulder but which fade on the ventral part of the whorl and are missing over the venter, at least at larger diameters. As growth proceeds they become more distant, only eight being present on the last preserved whorl in C.83500. The strength of the ribs does not increase appreciably during ontogeny and hence the inner whorls appear more coarsely ornamented than the outer.

REMARKS. The present material is closely comparable to *Pachydiscus* (*P.*) *egertoni* (Forbes). The lectotype (C.51038, see Forbes 1846: pl. 9, fig. 1; sel. Matsumoto 1959: 42, text-fig. 17) differs only in its slightly greater whorl compression and rather more prominent umbilical bullae. *P.* (*P.*) *neubergicus* (Hauer 1858: 12; pl. 2, figs 1, 2; pl. 3, figs 1, 2) is similar but retains minor ventral ribbing in the later stages and shows major ribs continuous over the venter. The latter are, however, most pronounced on the dorsal half of the whorl as in *P.* (*P.*) *egertoni.*

Part of a juvenile whorl described by Reyment (1955: 17; 1957: 63; pl. 11, figs 2a, 2b), from a horizon of the same age near Afikpo to the north-west of Calabar, is probably conspecific with the present material. Reyment placed this individual in *Pachydiscus* aff. *stallauensis* Imkeller. Its ribbing is similar in style to that in the present material, although both major and minor ribs are present and its whorl section is a little less compressed. These, however, are probably juvenile features, being similar to those of the early stages in *P.* (*P.*) *egertoni* where minor ventral ribs are present in the lectotype and in a specimen described by Kossmat (1898: 159; pl. 21, figs 4a–c). The adult whorls in *P.* (*P.*) *stallauensis* differ from those in the present material in showing denser but more feeble ribs (see Imkeller 1901: pl. 3, fig. 5).

Pachydiscus (Pachydiscus) dossantosi (Maury, 1930)

Figs 17, 18, 20

1930 *Parapachydiscus dossantosi* Maury: 136; pl. 16, fig. 1; pl. 17, figs 1, 2.
? 1944 *Parapachydiscus* sp. Olsson: 107; pl. 16, fig. 1.

MATERIAL AND OCCURRENCE. Twenty-five specimens (C.82125–6, C.82151–4, C.82176, C.83205–8, C.83506–7, C.85269, UIN 437.1–11) from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar.

DESCRIPTION. The shell reaches a diameter of at least 220 mm and is fairly evolute, about half the previous whorl being covered. In the early stages the whorls are only a little higher than broad with convexly rounded flanks and a rounded venter. Whorl height increases more rapidly than whorl breadth so that in the later stages the whorls are distinctly compressed with rather flattened flanks and a broadly arched venter.

There are approximately 42 ribs per whorl in the middle stages. Most are short, extending over the ventral third to half of the whorl, and are concealed by the succeeding whorl. Every second to fourth rib is extended to the umbilical shoulder. These major ribs attain their greatest development on the dorsal third of the flank and are sometimes very faint, almost interrupted, in the middle part of the flank. On internal moulds the ribs are interrupted to a greater or lesser extent along the venter by a siphonal groove. Towards adulthood the intercalated ventral ribs become fewer, from generally two or three to only one or two.

REMARKS. In general morphology this material is close to certain of the north-west European Lower Maastrichtian pachydiscids, particularly *Pachydiscus* (*P.*) *gollevillensis* (d'Orbigny). In that species, however, the ornament usually consists of discrete umbilical bullae and ventral ribs which are finer and more numerous than in the Nigerian specimens. In some examples the umbilical bullae may extend across the flanks and join the ventral ribs (see, for example, Grossouvre 1894: pl. 29, figs 4a, 4b), such individuals coming to resemble the

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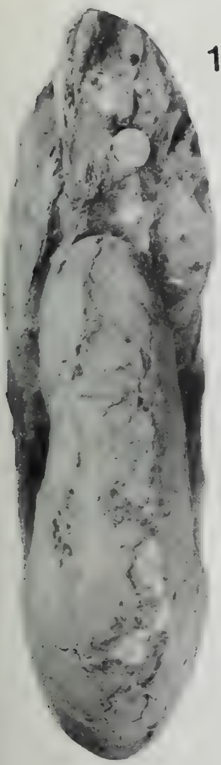
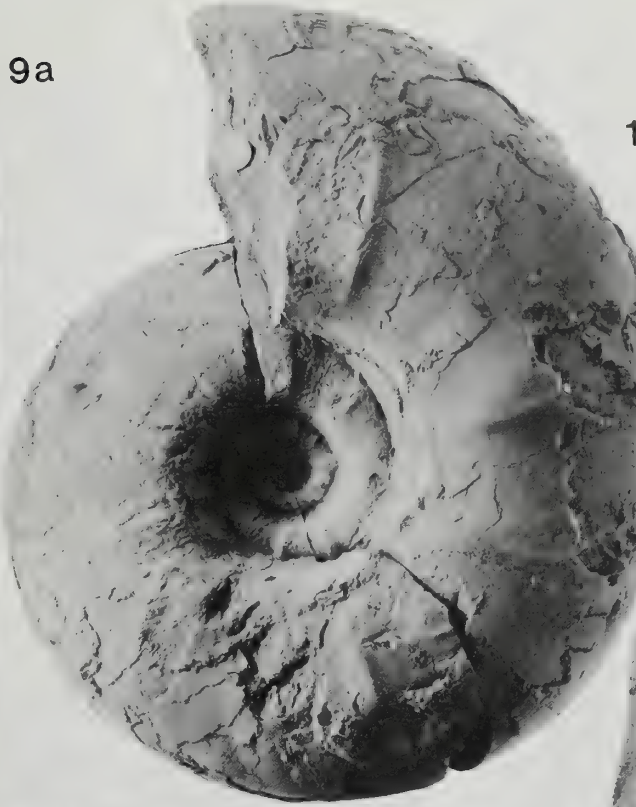
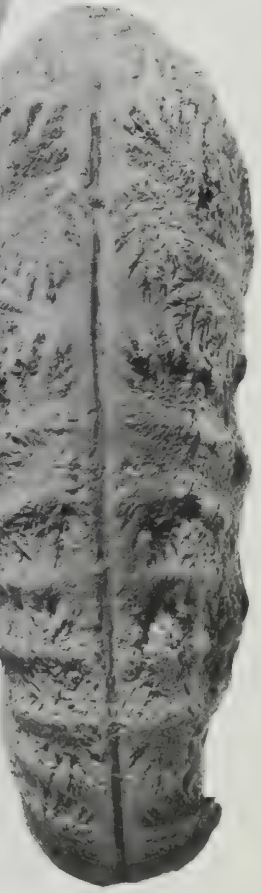
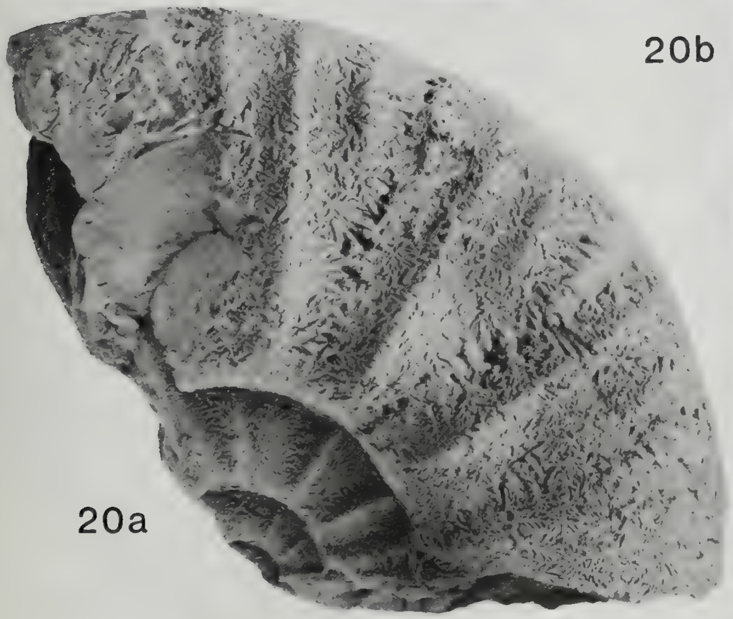
Fig. 19a, b *Pachydiscus (Pachydiscus) egertoni* (Forbes). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83500, ×0·75.

Fig. 20a, b *Pachydiscus (Pachydiscus) dossantosi* (Maury). Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. C.85269, ×1. See also Figs 17, 18.


19a


19b


20b


20a

present material. A similar trait exists in specimens from the United States related to *P.* (*P.*) *gollevillensis* (Young 1963: pl. 14, figs 2, 3). *P.* (*P.*) *neubergicus* (Hauer) may also show this type of ornament (Hauer 1858: pl. 2, figs 1, 2; Grossouvre 1894: pl. 26, fig. 3a; pl. 38, fig. 3), but has a more compressed shell, while *P.* (*P.*) *jacquoti* Seunes (1890: pl. 2, figs 1–3; pl. 3, figs 4a, 4b), also with this ornamental style, has rather inflated whorls.

Most closely comparable with the Nigerian material is *P.* (*P.*) *dossantosi* (Maury 1930: 136; pl. 16, fig. 1; pl. 17, figs 1, 2) from eastern Brazil. This species has an overall morphology and ornament of precisely the same type as the present material, and also shows a reduction in the number of intercalated ribs towards adulthood. Two other Brazilian species, *P.* (*P.*) *gettyi* (Maury 1930: 138; pl. 14, figs 1, 2) and *P.* (*P.*) *endymion* (Maury 1930: 156; pl. 32), are close to *P.* (*P.*) *dossantosi* and may be synonyms. A *Pachydiscus* from Peru described by Olsson (1944: 107; pl. 16, fig. 7) is also very similar to *P.* (*P.*) *dossantosi*.

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894

Family **FORBESICERATIDAE** Wright, 1952

Genus ***FORBESICERAS*** Kossmat, 1897

TYPE SPECIES. *Ammonites largilliertianus* d'Orbigny, 1841; by the subsequent designation of Diener, 1925.

Forbesiceras subobtectum (Stoliczka, 1864)

Fig. 21a, b

1864 *Ammonites subobtectus* Stoliczka: 96; pl. 49, figs 2, 2a, 2b.
1964 *Forbesiceras subobtectum* (Stoliczka) Collignon: 62; pl. 335, fig. 1501.

MATERIAL AND OCCURRENCE. A single specimen (C.83430) from the Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar.

REMARKS. This specimen reaches a diameter of some 180 mm. The outer whorl shows a broad venter but is otherwise poorly preserved. Between diameters of about 60–80 mm the specimen shows an ornament typical of this species (see Stoliczka 1864: pl. 49, fig. 2), with a broad venter bordered on each side by a row of coarse tubercles with fine transverse ribbing between. The dorsal part of the flank bears pronounced prorsiradiate ribs terminating in coarse nodes in the mid-flank region, while there are coarse moderately rursiradiate ribs on the ventral third of the flanks.

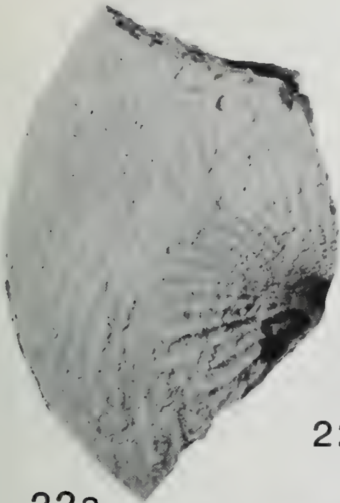
Forbesiceras obtectum (Sharpe, 1853)

Figs 22–25, 29

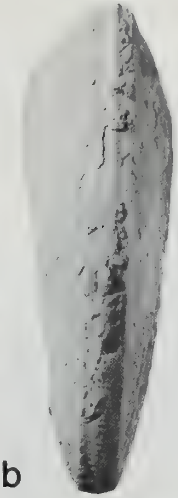
1853 *Ammonites obtectus* Sharpe: 20; pl. 7, figs 4a–c.
1907 *Forbesiceras obtectum* (Sharpe) Pervinquière: 108; pl. 6, figs 7–11.
1928 *Forbesiceras obtectum* (Sharpe); Collignon: pl. 2, figs 13, 13a.
1929 *Forbesiceras obtectum* (Sharpe); Collignon: 27.
1940 *Forbesiceras obtectum* (Sharpe); Fabre: 222; pl. 5, fig. 14.
1971 *Forbesiceras obtectum* (Sharpe); Kennedy: 47; pl. 9, figs 3a, 3b; pl. 16, fig. 3; pl. 46, fig. 3 (with synonymy).
1973 *Forbesiceras obtectum* (Sharpe); Cooper: 48; figs 5, 6A, 6B.
1976 *Forbesiceras obtectum* (Sharpe); Juignet & Kennedy: 82; pl. 5, figs 9a, 9b, 10a, 10b; pl. 6, figs 2a, 2b, 3a–c, 4, 5.

Fig. 21a, b *Forbesiceras subobtectum* (Stoliczka). Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar. C.83430, ×1.

Figs 22, 23 *Forbesiceras obtectum* (Sharpe). Odukpani Formation (Middle Cenomanian). Fig. 22a, b, from an uncertain locality, Calabar–Ikot Ekpene road. C.82148, ×1. Fig. 23a, b, 29·3 km from Calabar. C.83107, ×0·65. See also Figs 24, 25, 29.



22a



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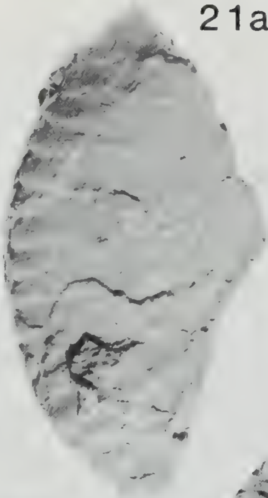
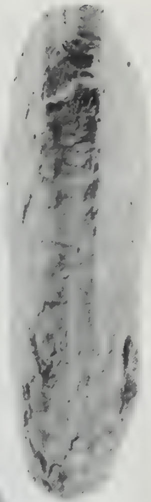


21a



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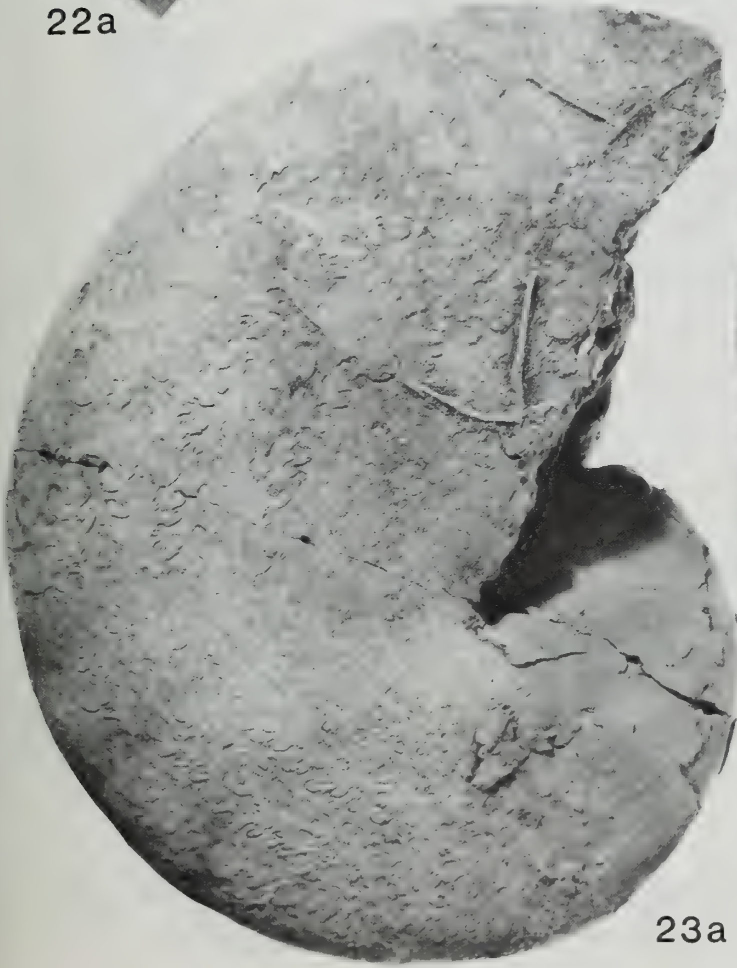
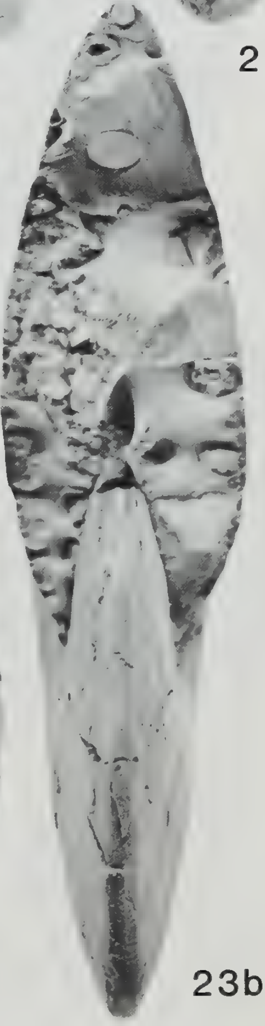


23a



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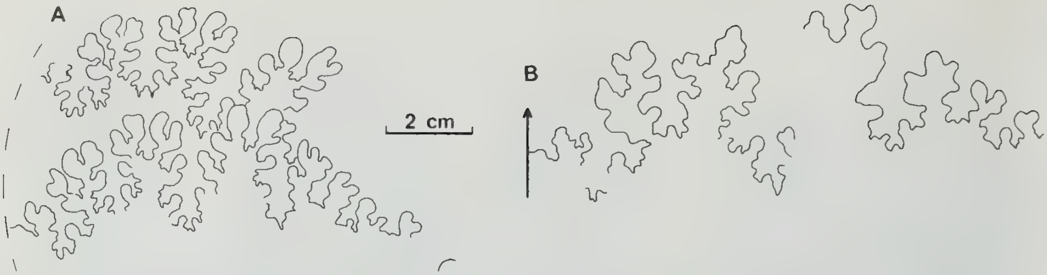

Fig. 24 Sutures in *Forbesiceras obtectum* (Sharpe). A, C.83107 at diameter of 165 mm; B, C.83549.

MATERIAL AND OCCURRENCE. Seven specimens (C.82112, C.82114, C.82148–9, C.83107, C.83476, C.83549) from the Odukpani Formation (Middle Cenomanian) can be definitely referred to this species. C.83107 is from a horizon exposed 29·3 km from Calabar, C.83476 and C.83549 from 30·3 km from Calabar: the remainder cannot be precisely localized. In addition two fragmentary specimens (C.83475, UIN 474.1) from 30·1 km from Calabar probably belong in this species.

DIMENSIONS.	D	Wb	Wh	U
C.83107	205	46 (22·4)	125 (61)	–
	155	36 (23)	100 (64·5)	–
	92	20 (22)	55 (60)	–

DESCRIPTION. The present material falls into two groups. Up to a diameter of some 80 mm development in both groups is similar, the ornament consisting of prorsiradiate ribs on the dorsal part of the flanks terminating in a row of bullate swellings or discrete tubercles in the middle of the flanks, while the ventral half of the flanks bear rursiradiate ribs terminating in fine clavate tubercles at the ventrolateral shoulder. The venter is narrowly fastigiate with dense nodate to bullate siphonal tubercles. The ornament at this stage is usually fairly pronounced.

At diameters in excess of 80 mm, however, development in the two groups differs markedly. The first group, represented by C.82112 (Fig. 29a, b), reaches full adult size at a diameter of some 110 mm, at which stage the sutures are simplified and approximated and the umbilicus is egressing, and the ornament is reduced in strength. The ribs are continuous from umbilicus to venter and are only slightly prorsiradiate on the dorsal part of the flanks and only slightly rursiradiate on the ventral part. The venter becomes broadly rounded with only a slight keel evident on the internal mould. The last third of the final whorl on this specimen is body chamber. It bears a broad deep pre-oral constriction swept forwards on the dorsal part of the flank and backwards on the ventral part.

The second group is more fully represented in the present collection (C.83107, C.83476, C.83549 and probably C.83475 and UIN 474.1; Figs 23a, b, 25a, b). Its members attain a very large size, the diameter of the phragmocone exceeding 250 mm. The strength of the ornament is also reduced during growth. At diameters of about 100 mm it is possible to make out weak prorsiradiate ribs on the dorsal part of the flanks and discontinuous rursiradiate ribs on the ventral part. At larger diameters, however, at least on internal moulds, the flanks appear perfectly smooth. At a diameter of 100 mm the venter appears narrowly fastigiate

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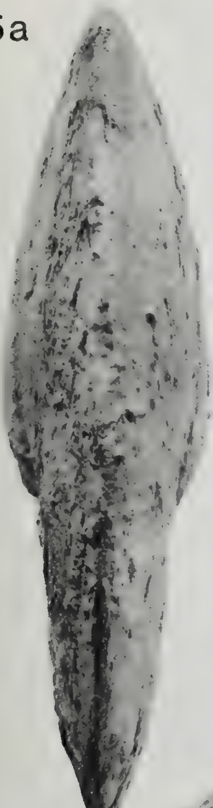
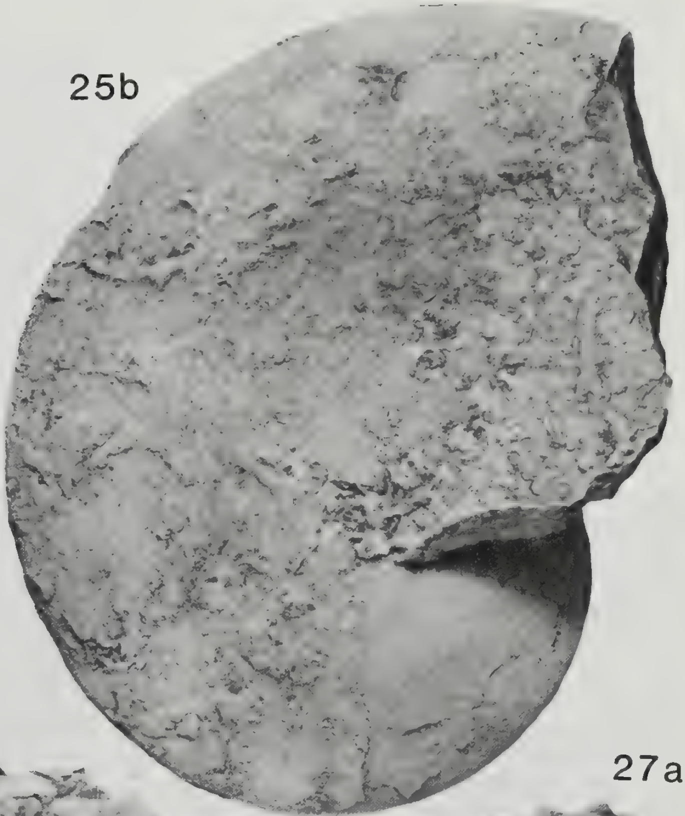
Fig. 25a, b *Forbesiceras obtectum* (Sharpe). Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar. C.83476, ×0·65. See also Figs 22–24, 29.

Figs 26–28 *Sharpeiceras laticlavium nigeriense* subsp. nov. Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1·5 km north of junction with Calabar–Ikot Ekpene road. Fig. 26, paratype C.83542, ×1. Fig. 27a, b, **holotype** C.83544, ×1. Fig. 28a, b, paratype C.83545, ×1. See also Fig. 31.

25a



25b



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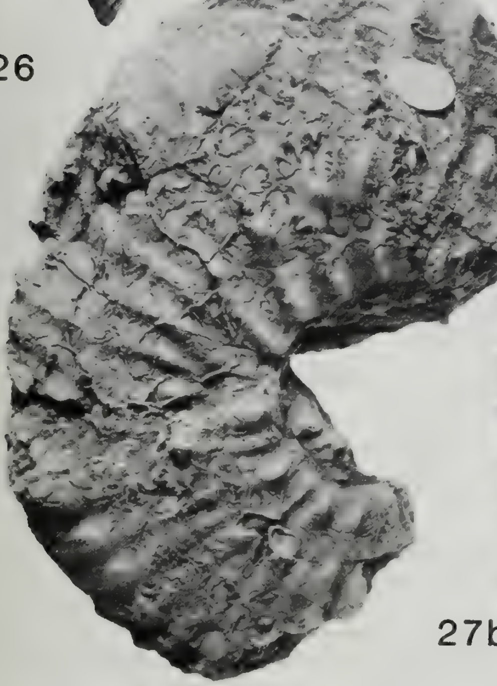
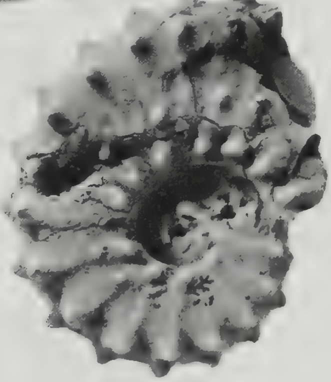
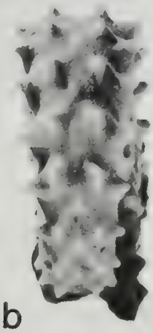


27a



27b



28a

28b

where the test is preserved, though on internal moulds it is sharply rounded at this and larger diameters. The suture pattern is variable in its details (Fig. 24). The saddles may become highly elongated with phylloid endings. The sutures may be crowded and overlapped, even at intermediate diameters.

Remarks. The two groups of this form described above appear to represent the microconch and macroconch of a dimorphic species. The large individuals of the second group conform closely with huge specimens which Cooper (1973: 48–49) found to be common in the Middle Cenomanian near Novo Redondo, Angola. *Forbesiceras obtectum* also occurs in southern England but is rare. Juignet & Kennedy (1976: 82–83) divided this material into two groups. The first, exemplified by the specimens figured by Kennedy (1971: pl. 16, fig. 3; pl. 46, fig. 3), shows finely ornamented, almost smooth adult whorls. These forms are comparable to the large Nigerian specimens. The second group, exemplified by the specimen figured by Kennedy (1971: pl. 5, figs 9a, 9b), contains forms grossly ornamented to a large size with a broad venter carrying coarse ventrolateral and siphonal tubercles. Intermediate forms from the low Middle Cenomanian Rouen fossil bed in north-west France were described by Juignet & Kennedy (1976: pl. 5, figs 10a, 10b; pl. 6, figs 2a, 2b). Nothing in the Nigerian collection is closely comparable to Juignet & Kennedy's second group, which appears to be intermediate between *F. subobtectum* (Stoliczka) and *F. obtectum*. In the Odukpani Formation horizons known to contain *F. obtectum* lie above that with *F. subobtectum*. It is possible that reduction in strength of the ornament and breadth of the venter are stratigraphic trends in this group of *Forbesiceras*. The differences between the two Nigerian groups of *F. obtectum* described here, however, seem to be due to dimorphism.

Two large specimens of *Forbesiceras* (C.83548, UIN 475.1), both reaching a diameter of some 250 mm, come from the lower part of the Odukpani Formation at 25·8 km from Calabar, and consist only of the outer whorl. They resemble the large specimens of *F. obtectum* described above, but in the absence of the inner whorls cannot be identified to species level. Species of *Forbesiceras* from various levels in the Cenomanian are closely alike at large diameters, showing smooth compressed whorls with a sharply rounded venter. *F. largilliertianum* (d'Orbigny), which occurs in the Lower Cenomanian of southern England (Kennedy & Hancock 1978), has such an adult morphology (see Sharpe 1853: pl. 7, figs 1a, 1b), as does *F. conlini* Stephenson (1952: 205; pl. 56, fig. 1; pl. 57, figs 2–6) from the Middle Cenomanian of Texas. Material from the late Cenomanian of western France referred to *F.* aff. *largilliertianum* by Kennedy, Juignet & Hancock (1981: 39; figs 7, 10A) is also of this form at large sizes.

Family **ACANTHOCERATIDAE** Grossouvre, 1894

Subfamily **MANTELLICERATINAE** Hyatt, 1903

Genus ***SHARPEICERAS*** Hyatt, 1903

Type species. *Ammonites laticlavius* Sharpe, 1855; by original designation of Hyatt, 1903.

Sharpeiceras laticlavium (Sharpe) ***nigeriense*** subsp. nov.

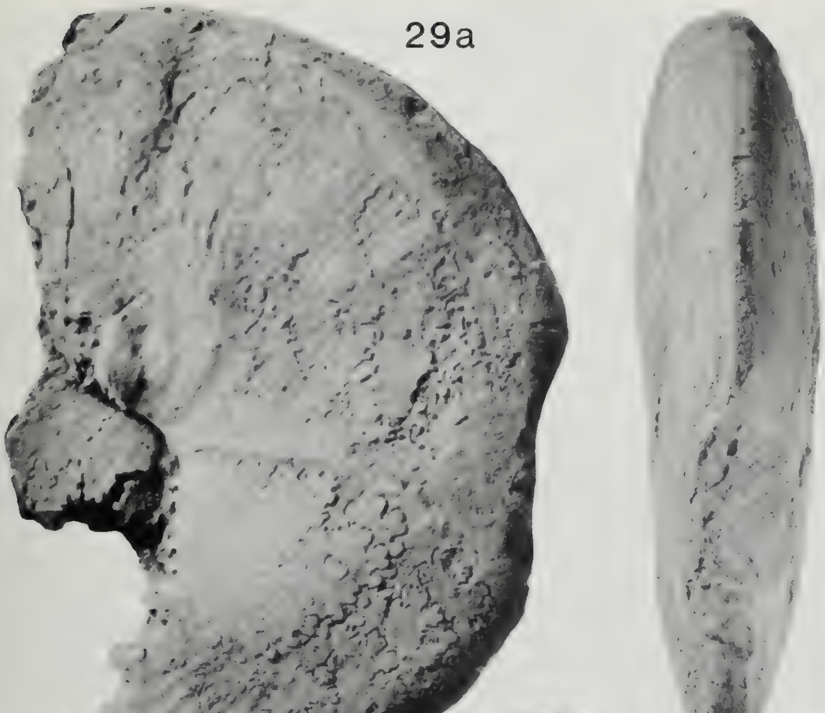
Figs 26–28, 31

Holotype. C.83544, showing the juvenile whorls (Fig. 27a, b). From the Odukpani Formation (Lower Cenomanian), cutting on the Calabar–Akamkpa road, 1·5 km north of the junction with the Calabar–Ikot Ekpene road.

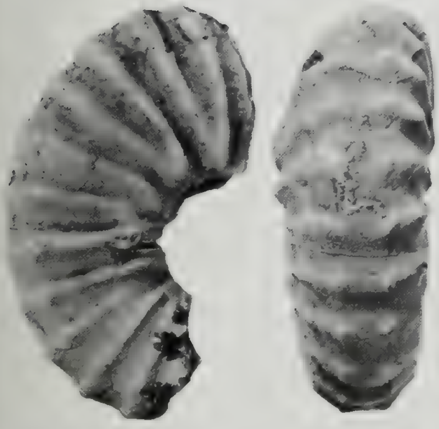
Paratypes. C.83542–3, C.83545, UIN 500.1, all from the same locality as the holotype.

Name. From Nigeria.

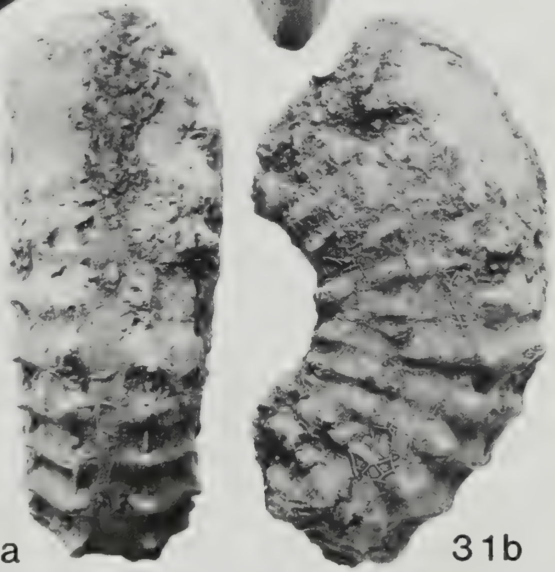
Diagnosis. *Sharpeiceras* with distant ribs and spinose inner and outer ventrolateral tubercles in the early stages, but with closely-spaced ribbing and subdued tuberculation in the middle stages. Both major and minor ribs present throughout.



29a 29b



30a 30b



31a 31b

Fig. 29a, b *Forbesiceras obtectum* (Sharpe). Odukpani Formation (Middle Cenomanian), from an uncertain locality, Calabar–Ikot Ekpene road. C.82112, an adult micoconch, ×1. See also Figs 22–25.

Fig. 30a, b *Acompsoceras calabarense* sp. nov. Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1·5 km north of junction with Calabar–Ikot Ekpene road. Paratype C.83553, ×1. See also Fig. 32.

Fig. 31a, b *Sharpeiceras laticlavium nigeriense* subsp. nov. Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1·5 km north of junction with Calabar–Ikot Ekpene road. Paratype C.83543, ×1. See also Figs 26–28.

DESCRIPTION. The shell is moderately evolute with high, flattened whorl sides. The largest specimen (C.83542), fully septate, attains a diameter of some 110 mm.

At a diameter of 15 mm there are 15 low, narrow, rounded ribs in each whorl. Each rib bears prominent inner and outer ventrolateral tubercles. On the flank the ribs are alternately long and short. The former terminate in low bullate umbilical tubercles, the latter die out in the middle part of the flank.

In the complete whorl between diameters of 22 and 55 mm there are 18 rows of pronounced spinose inner and outer ventrolateral tubercles. Ten of these rows are associated with long, narrow, rounded ribs which cross the flank and terminate in well-developed conical umbilical tubercles. The remainder are borne upon shorter ribs which terminate in the middle or dorsal half of the flank. At a diameter of 30 mm mid-lateral tubercles appear. At first they are close to the umbilical shoulder, but they gradually migrate ventrally taking up a position just dorsal of the middle of the flank. The short ribs generally lack mid-lateral tubercles. In the early stages the whorls are markedly higher than broad, with a rather narrow venter.

As growth proceeds the ventrolateral and umbilical tubercles become subdued while rib density increases markedly. In the half whorl between diameters of about 65 and 110 mm in C.83542 there are approximately 18 rounded ribs of width equal to that of the interspaces. Most of these ribs arise at a variably pronounced, bullate or pointed, umbilical tubercle and bear a prominent mid-lateral tubercle and weaker inner and outer ventrolateral tubercles which may tend to fuse into a bullate swelling crossing the ventrolateral shoulder. Intercalated ribs, also bearing inner and outer ventrolateral tubercles, are present. Some die out ventral of the mid-lateral tubercles, others bear a subdued mid-lateral tubercle and terminate just dorsal of the umbilical shoulder. Occasionally, ribs bifurcate at the mid-lateral tubercles. At this stage whorl height exceeds whorl breadth but the venter is wide and flat, being bordered by sloping ventrolateral shoulders.

The suture is complex with E and L deep and highly subdivided while the saddles exhibit subphylloid endings.

REMARKS. This *Sharpeiceras* has a distinctive ontogenetic development and is easily distinguished from most previously described species. *S. schlueteri* (Schlüter 1871: 18; pl. 7, figs 4–9; Hyatt 1903: 111) is more evolute with coarser ribbing in the middle stages. *S. vohipalense* Collignon (1964: 104; pl. 354, fig. 1565) also shows stronger ribbing in the middle stages, at which the inner ventrolateral tubercles become exaggerated rather than subdued. *S. occidentale* Benavides-Cáceres (1956: 465; pl. 54, figs 5, 6) is more compressed in its later stages with a coarser decoration. *S. congo* Matsumoto, Muramoto & Takahashi (1969: 261; pl. 29, fig. 1; pl. 30, fig. 1) has coarse distant ribbing throughout ontogeny with massive tuberculation developing in the later stages. *S. florencae* Spath (1925: 198; pl. 37; Kennedy 1971: 67; pl. 25, fig. 2) has a more depressed whorl section and coarser ornament in the middle stages. *S. tlahualiloense* (Kellum & Mintz 1962: 276; pl. 6, fig. 1; pl. 7, figs 1, 2; pl. 8, fig. 1) is similar to *S. florencae* and may be a synonym (see also Juignet & Kennedy 1976: 100). *S. corroyi* (Fabre 1940: pl. 7, figs 5, 6) is more evolute and compressed with a rounded venter and broad ribbing. *S. piveteaui* Collignon (1928–29: 37; pl. 3, figs 18, 18a) is a nucleus of less than 20 mm diameter impossible to compare with other material. *S. falloti* (Collignon 1931: 41; pl. 4, figs 9–12) is also based on juvenile specimens. They resemble the early whorls in *S. laticlavium nigeriense* although they seem to have a somewhat greater rib density at diameters of less than 20 mm. The two may be closely related but ignorance of the later whorls makes detailed comparison impossible. Undoubtedly close to the present material is *S. laticlavium* (Sharpe), of which *S. goliath* Haas (1942: 7, fig. 7) is a synonym (see Kennedy 1971: 66; Cooper 1978*a*: 6). The holotype (Sharpe 1855: pl. 14, figs 1a, 1b; Kennedy 1971: pl. 27, figs 1a–c) has a very similar gross morphology and ornament in its middle stages. Its ventrolateral tubercles lack the early spinosity of those in the Nigerian material but this is probably an effect of preservation. The ornament of the early whorls is unclear in the holotype, as it is in conspecific French material described by Juignet &

Kennedy (1976: 99; pl. 10, figs 1, 2). Rib density here, however, seems to be greater than in the Nigerian form, this being the major difference between the two. In view of their overall similarity, however, they are separated here at the subspecific level only. *S. laticlavium* var. *indica* (Kossmat 1895: 103; pl. 10, figs 5, 6) also has a similar ontogenetic development, but again the ribs are more closely spaced in the early stages and less crowded at diameters of 100 mm or so, at which stage the whorls are more compressed. In *S. laticlavium* var. *mexicanum* Böse (1927: 253; pl. 10, fig. 6; pl. 11, fig. 1) the ribs are said to spring in pairs from the umbilical tubercles, this form also being rather highly compressed.

Genus *ACOMPSOCERAS* Hyatt, 1903

TYPE SPECIES. *Ammonites bochumensis* Schlüter 1871; by the original designation of Hyatt, 1903.

Acompsoceras calabarense sp. nov.

Figs 30, 32

HOLOTYPE. C.85250, about half a whorl (Fig. 32a, b). From the Odukpani Formation (Lower Cenomanian), cutting on the Calabar–Akamkpa road, 1·5 km north of the junction with the Calabar–Ikot Ekpene road.

PARATYPES. C.83552–3, C.85249, C.85251, all from the same locality as the holotype.

NAME. After the town of Calabar, close to the locality of the type material.

DIAGNOSIS. *Acompsoceras* with coarse, alternately long and short ribs. Umbilical tubercles large and bullate, inner ventrolateral tubercles prominent and rounded, outer ventrolateral tubercles markedly clavate. Mid-lateral tubercles absent.

DESCRIPTION. The holotype consists of approximately half a whorl with a diameter of 100 mm. It displays 11 broad rounded ribs, alternately long and short. The long ribs carry pronounced, highly bullate umbilical tubercles, prominent rounded inner ventrolateral tubercles and markedly clavate outer ventrolateral tubercles. The short ribs lack, or display only weakly-developed, umbilical tubercles. The venter is narrow and flat. There are no mid-lateral tubercles. The whorls in the holotype are rather compressed with flattened flanks converging slightly ventrally. A smaller specimen (C.83553, Fig. 30a, b) shows a broader pentagonal whorl section at a diameter of some 40 mm. At this stage the ribs are narrower and sharper.

REMARKS. This *Acompsoceras* is easily distinguished from most previously described species by its very coarse ornament. *A. pseudosarthense* Collignon (1964: 108; pl. 356, fig. 1568), *A. tenue* Collignon (1964: 110; pl. 357, figs 1572, 1573), *A. catzigrasae* (Collignon (1964: 112; pl. 358, fig. 1577), *A. sahnii* Collignon (1964: 111; pl. 358, figs 1575, 1576) and *A. viotti* Collignon (1966: 26; pl. 16, fig. 1) all have finer, denser, ribbing. *A. antsatramahaveloense* Collignon (1964: 109; pl. 357, fig. 1571) has broader more rectangular whorls. *A. essendiense* (Schlüter 1871: 3; pl. 1, figs 5–7; pl. 2, fig. 2) has a very feeble umbilical and ventrolateral ornament which disappears later in ontogeny. *A. renevieri* (Sharpe 1857: 44; pl. 20, figs 2a–c; Kennedy 1971: 68; pl. 30, figs 1a–c) lacks well-developed ribbing and inner ventrolateral tubercles. A specimen from the Odukpani Formation referred by Reyment (1957: 60; pl. 8, figs 3a, 3b) to *A. subwaterloti* Venzo shows broader, flatter ribbing and sharper ventrolateral tubercles. It displays mid-lateral tubercles but lacks inner ventrolateral tubercles. The same style of ribbing is shown by the holotype of *A. subwaterloti* (Venzo 1936: 87; pl. 7, figs 11a, 11b). It also lacks inner ventrolateral tubercles, but this is a very small specimen making detailed comparison difficult. Closest to the present material is *A. sarthense* (Guéranger 1867: 5; pl. 4, fig. 1; pl. 8, fig. 2), which has a similar gross morphology and only slightly finer ornament (see Kennedy 1971: 67; pl. 26, fig. 3; pl. 29, figs 1a–c). This species, however, has mid-lateral tubercles and its umbilical tubercles are far less swollen and bullate than in *A. calabarense*.

Acompsoceras aff. ***renevieri*** (Sharpe, 1857)

Fig. 33a, b

Compare: 1857 *Ammonites renevieri* Sharpe: 44; pl. 20, figs 2a–c.
1971 *Acompsoceras renevieri* (Sharpe); Kennedy: 68; pl. 30, figs 1a–c (with synonymy).

Material and occurrence. Four specimens (C.83498, C.85248, UIN 482.1–2) from the Odukpani Formation (Lower? Cenomanian), cutting on the Calabar–Akamkpa road, 1 km north of the junction with the Calabar–Ikot Ekpene road.

Remarks. These specimens, which reach a large size, show sparse, broad, bulge-like ribs on the dorsal half of the flanks. The venter is bordered by numerous, fine, clavate ventrolateral tubercles. *Acompsoceras renevieri* (Sharpe) (see Kennedy 1971: 68; pl. 30, figs 1a–c) has a very similar ornament, although it has fewer and coarser ventrolateral tubercles. The two are closely related, but better material is needed to clarify the taxonomic status of the Nigerian form.

Genus ***PSEUDOCALYCOCERAS*** Thomel, 1969

Type species. *Ammonites harpax* Stoliczka, 1865; by the original designation of Thomel, 1969.

Pseudocalycoceras cf. ***haughi*** (Pervinquière, 1907)

Fig. 34a, b

1907 *Acanthoceras haughi* Pervinquière: 270; pl. 14, figs 1a, 1b.
1972 *Pseudocalycoceras* (*Haughiceras*) *haughi* (Pervinquière) Thomel: 97; pl. 131, figs 7, 8 (with synonymy).
1981 *Pseudocalycoceras haughi* (Pervinquière); Kennedy, Juignet & Hancock: 48.

Material and occurrence. A single specimen (C.82111) from an uncertain horizon in the Odukpani Formation (Upper Cenomanian), Calabar–Ikot Ekpene road.

Description. This specimen consists of just over one-third of a whorl. It has a pentagonal costal section while intercostally the flanks and venter are broadly rounded. The whorl is a little broader than high, the greatest intercostal breadth being at the level of the umbilical tubercle. There are seven narrow, rounded major ribs and three minor ribs on this specimen, the latter not reaching the umbilical shoulder. At the adapical end of the specimen each major rib carries a pair of unevenly developed knob-like umbilical tubercles, sometimes highly effaced, a pair of inner and outer ventrolateral tubercles and a weakly developed siphonal tubercle. All the tubercles are bullate. On the flanks the ribs are rursiradiate, they are bent forwards between the inner and outer ventrolateral tubercles and are noticeably concave between the opposing outer ventrolaterals. An occasional rib may arise at the umbilical shoulder on one side but terminate on the opposite flank before reaching this point. Ribs may spring in pairs from the umbilical tubercles. The minor ribs carry siphonal, inner and outer ventrolateral tubercles. At the adoral end of the specimen the siphonal and outer ventrolateral tubercles are very subdued but the umbilicals and inner ventrolaterals are still marked. Impressions upon the dorsum indicate that in the preceding whorl the outer ventrolateral and siphonal tubercles were more strongly developed.

Remarks. In its rather inflated whorls and relatively low rib density this specimen seems to be most closely comparable with *Pseudocalycoceras haughi* (Pervinquière 1907: 270; pl. 14,

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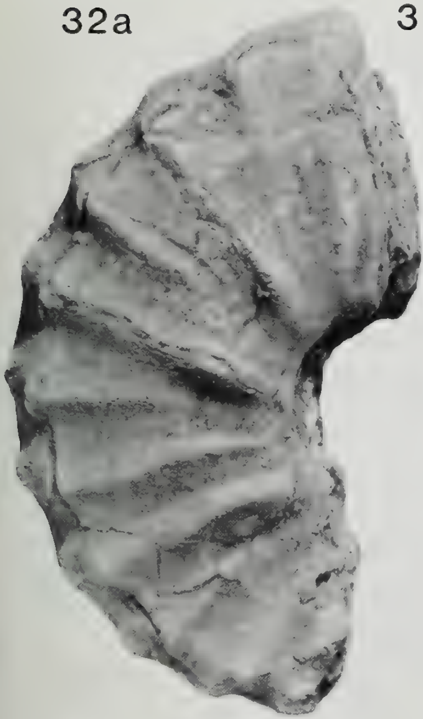
Fig. 32a, b *Acompsoceras calabarense* sp. nov. Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1·5 km north of junction with Calabar–Ikot Ekpene road. **Holotype** C.85250, ×1. See also Fig. 30.

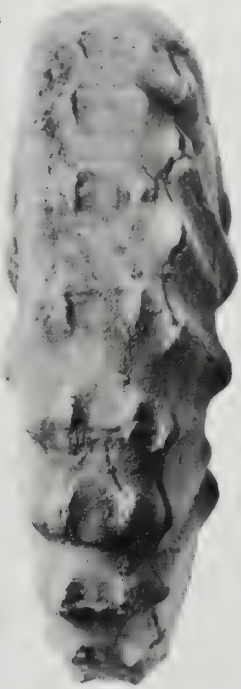
Fig. 33a, b *Acompsoceras* aff. *renevieri* (Sharpe). Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1 km north of junction with Calabar–Ikot Ekpene road. C.85248, ×1.

Fig. 34a, b *Pseudocalycoceras* cf. *haughi* (Pervinquière). Odukpani Formation (Upper Cenomanian), from an uncertain locality, Calabar–Ikot Ekpene road. C.82111, ×1.

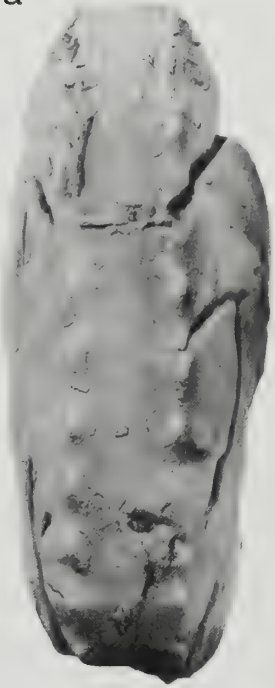
32a



32b



33a



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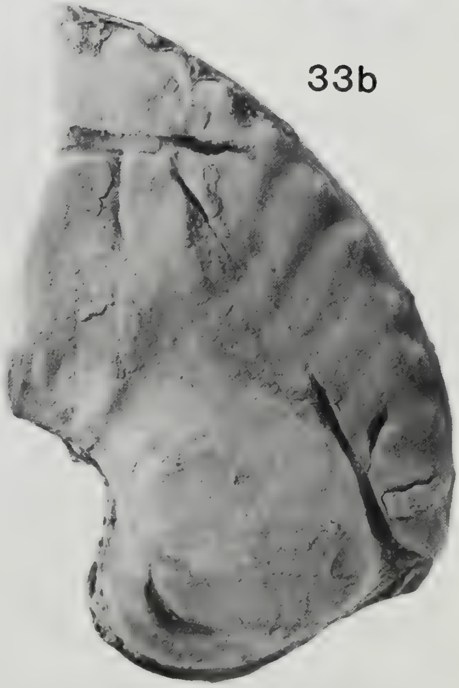

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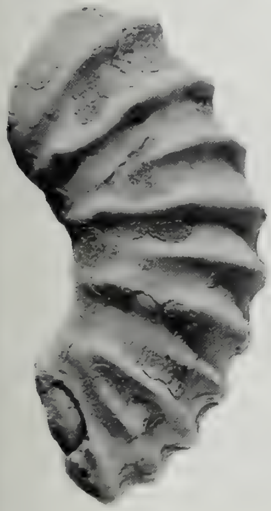
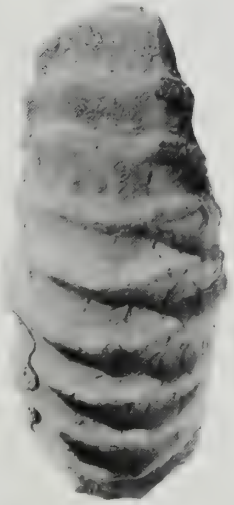


34b



figs 1a, 1b). Kennedy *et al.* (1981: 48), in the most recent review of this genus, gave a list of possible synonyms of *P. haughi.* Of these, *P. paralouitense* (Basse 1940: 449; pl. 7, fig. 4; pl. 8, figs 2, 3; pl. 9, fig. 3) shows a very similar style and strength of ribbing, with the ribs bent back strongly over the venter just as in the Nigerian specimen. Although generally with narrower whorls, some examples of *P. paralouitense* may approach the breadth of the present specimen (see Basse 1940: pl. 9, fig. 3).

P. angolaense (Spath) (see Cooper 1978: 96) and the similar *P. dentonense* (Moreman) (see Cobban & Scott 1972) both show less inflated whorls with broader denser ribbing. *P. harpax* (Stoliczka 1865: 72; pl. 39, fig. 1) and *P. morpheus* (Stoliczka 1865: pl. 38, fig. 1) both have an ovoid compressed whorl section with the inner and outer ventrolateral tubercles closer together. The former is, in addition, much more densely ribbed.

Genus ***CALYCOCERAS*** Hyatt, 1900

Subgenus ***NEWBOLDICERAS*** Thomel, 1972

TYPE SPECIES. *Acanthoceras newboldi* Kossmat, 1897; by the original designation of Thomel, 1972.

Calycoceras (Newboldiceras) annulatum Collignon, 1964

Figs 35, 36

1964	*Calycoceras annulatum* Collignon: 127; pl. 366, figs 1597, 1598.
? 1972	*Calycoceras* (*Calycoceras*) sp. aff. *annulatum* Collignon; Thomel: 64; pl. 16, figs 6, 7; pl. 18, figs 1, 2.
? 1973	*Calycoceras annulatum* Collignon; Cooper: 54, figs 8A–C.
? 1978*a*	*Calycoceras* (*Conlinoceras*) *annulatum* Collignon; Cooper: 6.

MATERIAL AND OCCURRENCE. A single specimen (C.83477) from the Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83477	166	54 (32·5)	54 (32·5)	70 (42)
	116	48 (41)	42 (36)	–

DESCRIPTION. This specimen, reaching a diameter of 166 mm, consists of an adult(?) body chamber. It is evolute, the whorls being a little broader than high adapically but with whorl breadth equal to whorl height adorally. Intercostally the whorls are broadly rounded. The costal section is pentagonal at the adapical end of the specimen while adorally it is more nearly rounded (Fig. 35). There are 17 narrow ribs in this approximate half whorl. Each

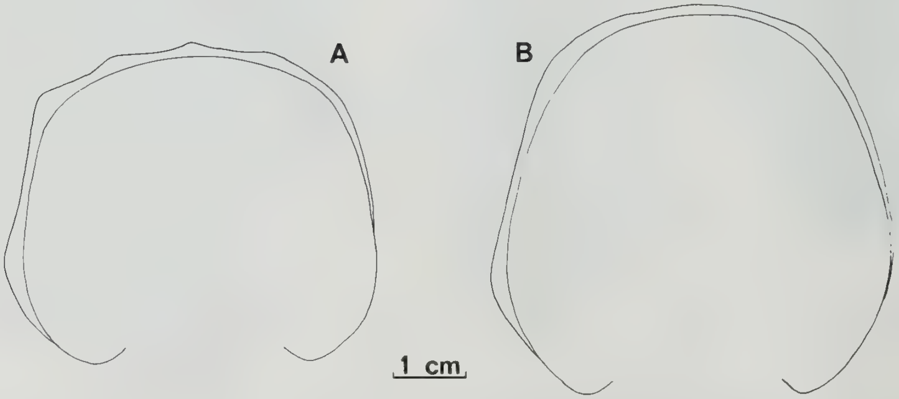


Fig. 35 Whorl sections in *Calycoceras (Newboldiceras) annulatum* Collignon. A, C.83477 at diameter of 115 mm; B, C.83477 at diameter of 160 mm.

originates on one side at a pronounced umbilical tubercle and bears on this side a fairly prominent inner ventrolateral tubercle. There are also subdued but definite outer ventrolateral tubercles and a siphonal tubercle at the adapical end of the specimen. On the opposite side, each rib lacks, or displays only a subdued, inner ventrolateral tubercle and dies out on the ventral part of the flank. Thus the ornament is markedly asymmetrical. Adorally the tubercles fade and at the largest preserved diameter only the umbilical tubercles are developed to any appreciable degree. At the adapical end of the specimen the ribs are rursiradiate and concave over the venter but adorally they are more nearly rectiradiate.

REMARKS. This specimen compares well with the Malagasy species *Calycoceras annulatum* Collignon (1964: 127; pl. 366, figs 1597, 1598), particularly in its wide umbilicus and narrow, distant ribs. Collignon reported the species from his 'Lower Cenomanian' (Zone of *Mantelliceras mantelli* and *Calycoceras newboldi*), but this zone seems to include younger Cenomanian for *C. newboldi* is characteristic of the Middle and Upper Cenomanian in north-west Europe (Kennedy & Hancock 1978: 15–16). *C. annulatum* has been referred to various of the subgenera proposed for *Calycoceras* by Thomel (1972) and Cobban & Scott (1972) (see reviews in Juignet & Kennedy 1976, Wright & Kennedy 1981). Thomel (1972: 64) included it in *C.* (*Calycoceras*) and Cooper (1978*a*: 6) in *C.* (*Conlinoceras*). Its closest affinities, however, seem to lie with *C.* (*Newboldiceras*) (type species *Acanthoceras newboldi* Kossmat 1897: 4; pl. 1, figs 2a, 2b, 3a–c; pl. 3, fig. 2) with which it agrees in its large size and persistent polygonal whorl section and tubercles. It differs from the type species in its wider umbilicus and more distant ribs, but an intermediate form has been described by Pervinquière (1907: 264; pl. 13, figs 1a, 1b).

Subfamily **ACANTHOCERATINAE** Grossouvre, 1894

Genus ***ACANTHOCERAS*** Neumayr, 1875

TYPE SPECIES. *Ammonites rhotomagense* Brongniart, 1822; by the subsequent designation of Grossouvre, 1894.

Acanthoceras robustum Crick, 1907

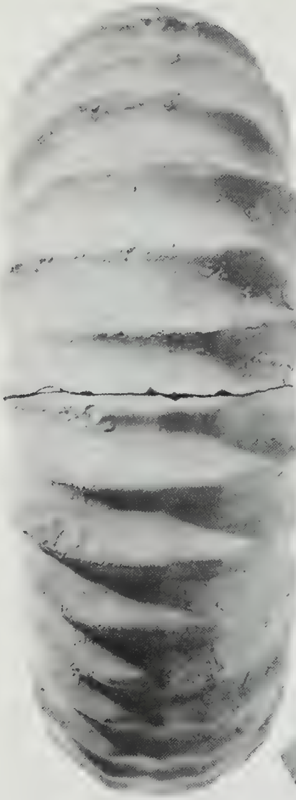
Fig. 37a, b

1907 *Acanthoceras robustum* Crick: 189.
1978 *Acanthoceras* sp. Kennedy: pl. 3, figs 6A, 6B.

MATERIAL AND OCCURENCE. A single specimen (C.83551) from the Odukpani Formation (Middle Cenomanian), 32·2 km from Calabar.

REMARKS. This fragment belongs in the group of *Acanthoceras rhotomagense* (Brongniart). It finds its closest counterparts, however, not within the basal Middle Cenomanian (*Turrilites costatus* Zone) type population of Rouen, north-west France (see Kennedy & Hancock 1970), but in the population from Zululand described by Crick (1907). Crick (1907) proposed a number of species names (*Acanthoceras flexuosum, A. crassiornatum, A. munitum, A. expansum, A. robustum, A. quadratum, A. hippocastanum* (*non* Sowerby) and *A. latum*) for members of this contemporaneous assemblage which differ only slightly from one another. As Kennedy (1971: 115–116; 1978: 22) has remarked, these forms probably represent variants of a single species. The present material agrees exactly in gross morphology and ornamentation with the variant given the name *A. robustum* by Crick (1907: 189). One (C.18189) of the three specimens (C.18188, C.18189 and C.18190, specimens 'a', 'b' and 'c' respectively in Crick 1907: 190) on which this species is based was figured by Kennedy (1978: pl. 3, figs 6A, 6B). When the Zululand fauna is revised *A. robustum* is likely to fall into synonymy.

The stratigraphic relationship between the Rouen and Zululand *Acanthoceras* populations is something of a problem. Although there is some morphological overlap (see Kennedy &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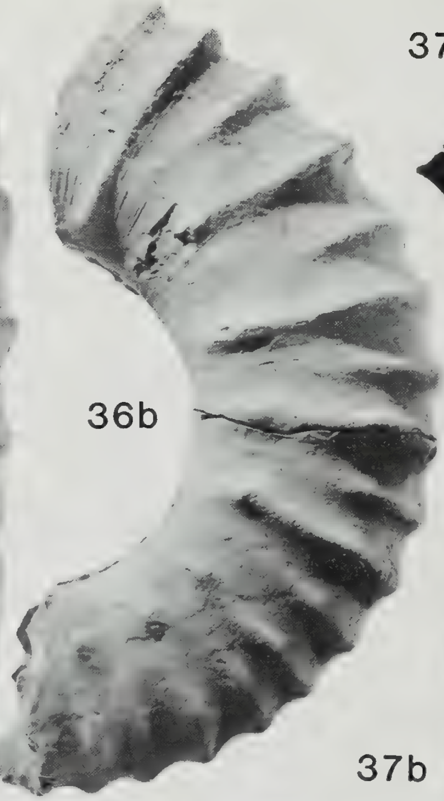
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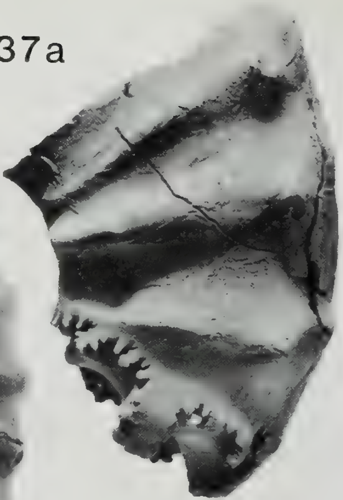
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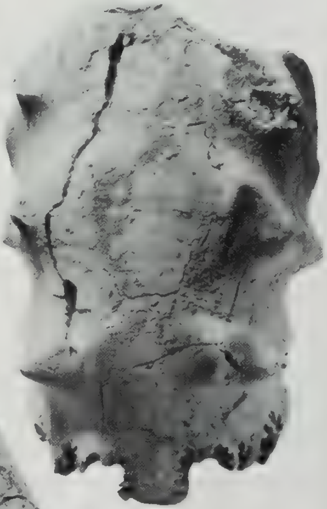
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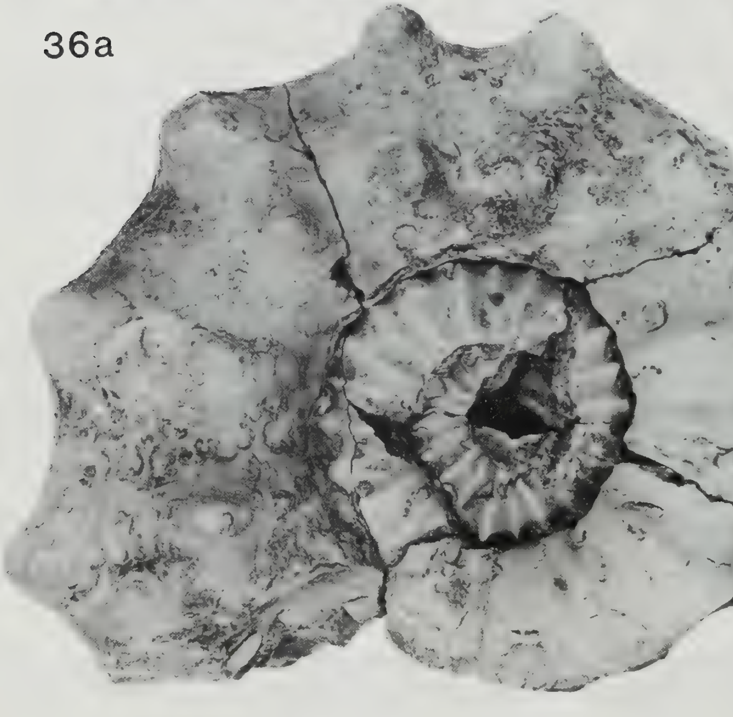
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Hancock 1970: 487), overall population structure is different. Partly on the basis of the associated *Calycoceras*, Kennedy (1971: 115–116) thought the Zululand fauna to be somewhat younger than that at Rouen, placing it above the *Turrilites acutus* assemblage as typically developed in southern England but below the overlying *Acanthoceras jukesbrownei* assemblage. In Zululand, however, the *Calycoceras* fauna occurs slightly above the one with *Acanthoceras* (Kennedy & Klinger 1975: 277; Kennedy 1978: 5), and Juignet & Kennedy (1976: 119) were undecided whether the differences between the Rouen and Zululand populations were the result of stratigraphical or geographical variation. In southern England the Zululand 'species' *A. latum* Crick occurs in the *T. acutus* Zone (Kennedy 1971: 89), occurring at a higher level than the Rouen fossil bed. The Nigerian specimen too occurs above beds exposed 27·9 km from Calabar which seem to correspond with the *T. costatus* Zone (see p. 59).

Acanthoceras amphibolum Morrow, 1935
Figs 38–41

1935 *Acanthoceras? amphibolum* Morrow: 470; pl. 49, figs 1–4, 6; pl. 51, figs 3, 4.
1952 *Acanthoceras hazzardi* Stephenson: 201; pl. 48, figs 1, 2; pl. 49, fig. 4.
1963 *Paracanthoceras amphibolum* (Morrow) Haas: 18.
1965 *Plesiacanthoceras amphibolum* (Morrow) Hattin: pl. 4, figs J, K; pl. 5, figs C–F.
1966 *Acanthoceras amphibolum* Morrow; Matsumoto & Obata: 45; text-figs 4–6.
1968 *Acanthoceras amphibolum* Morrow; Hattin: 1087.
1969 *Acanthoceras amphibolum* Morrow; Matsumoto, Muramoto & Takahashi: 266; pl. 31, figs 1a, 1b.
1972 *Acanthoceras amphibolum* Morrow; Cobban & Scott: 65; pl. 9; pl. 10, figs 12–16.
1977 *Acanthoceras amphibolum* Morrow; Cobban: 23; pl. 8, figs 8, 9; pl. 12, figs 10–12, 15–23.
1978 *Acanthoceras amphibolum* Morrow; Kauffman *et al.*: pl. 4, figs 1, 2.

MATERIAL AND OCCURRENCE. Nine specimens (C.83115, C.83117–8, C.83472–4, UIN 473.1–3) from the Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83472	215	72 (33·5)	70 (32·5)	90 (42)
C.83473	170	65 (38)	60 (35)	70 (41)
C.83118	135	56 (41·5)	51 (37·8)	56 (41·5)

DESCRIPTION. The shell is evolute and reaches a diameter in excess of 200 mm. The whorls are only a little broader than high, the flanks and the venter being flattened in early ontogeny but towards adulthood the flanks become slightly convex.

The earliest whorls are smooth and unconstricted. At a diameter of about 6 mm ribs, which carry rather prominent inner ventrolateral tubercles, appear on the flanks. The umbilical tubercles, which are inconsistently developed, are sometimes strong and bullate, sometimes highly effaced and often absent altogether. There are also outer ventrolateral and siphonal tubercles.

Between diameters of 26 and 70 mm the number of major ribs increases from about 14 or 15 to about 18 in each whorl. Each originates from a bullate, pointed umbilical tubercle, again often effaced to a greater or lesser degree. There is a pair of prominent inner ventrolateral tubercles, a pair of variably-developed outer ventrolaterals and a low clavate siphonal tubercle. The outer ventrolaterals are normally markedly clavate and often asymmetrical, with the steeper face at the adoral end, but sometimes they are conical or

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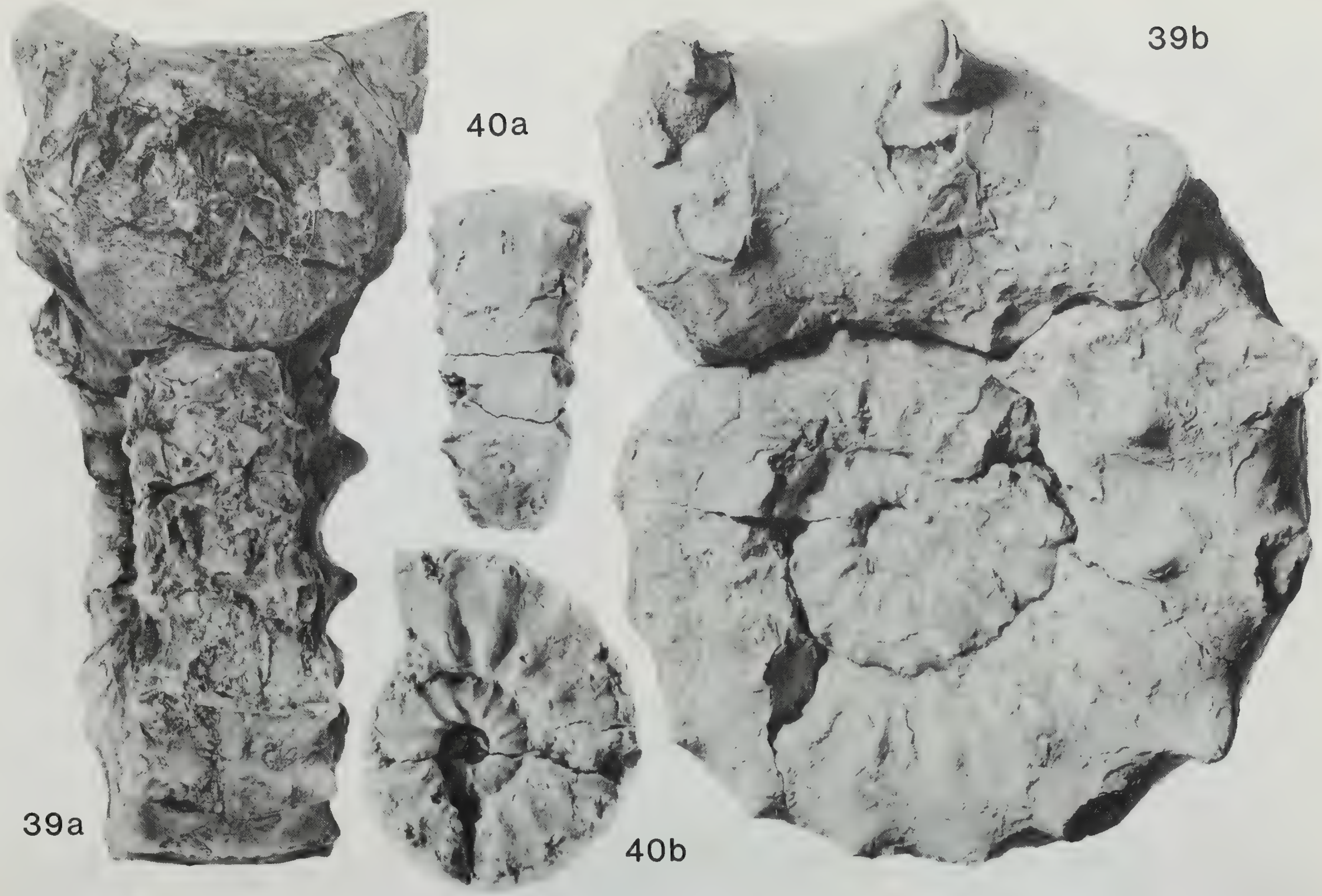
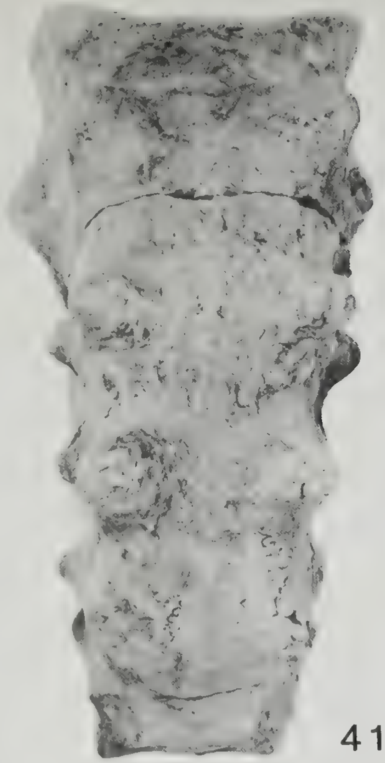
Fig. 36a, b *Calycoceras (Newboldiceras) annulatum* Collignon. Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar. C.83477, ×0·65. See also Fig. 35.

Fig. 37a, b *Acanthoceras robustum* Crick. Odukpani Formation (Middle Cenomanian), 32·2 km from Calabar. C.83551, ×0·75.

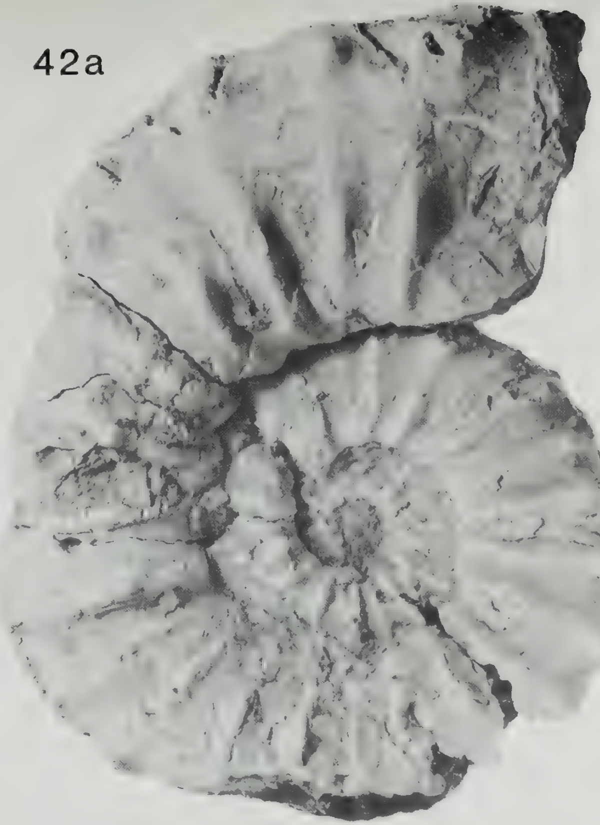
Fig. 38 *Acanthoceras amphibolum* Morrow. Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar. C.83473, ×0·65. See also Figs 39–41.



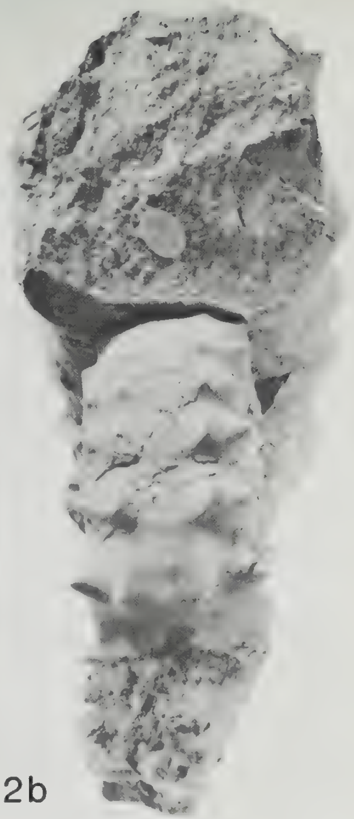
Figs 39, 40 *Acanthoceras amphibolum* Morrow. Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar. Fig. 39a, b, C.83472, ×0·65. Fig. 40a, b, C.83474, ×1. See also Figs 38, 41.



41



42a



42b

Fig. 41 *Acanthoceras amphibolum* Morrow. Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar. C.83473, ×0·65, ventral view of specimen shown in Fig. 38. See also Figs 39, 40.

Fig. 42a, b *Acanthoceras* sp. Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar. C.83116, ×0·75.

situated a little adoral of the inner ventrolaterals and connected to them by obliquely directed swellings. Intercalated at irregular intervals there are minor ribs bearing a siphonal tubercle and a pair of outer ventrolateral tubercles, and sometimes in addition a pair of inner ventrolaterals; they may extend some distance across the flank and approach the development of those major ribs carrying effaced umbilical tubercles.

At diameters in excess of 90 mm the outer ventrolateral and siphonal tubercles tend to fade, although low extended siphonal swellings may persist up to a diameter of some 120 mm forming an inconspicuous keel; broad low outer ventrolateral swellings may still occur at diameters of 100 mm or more. The number of ribs decreases at this stage: there are 12 to 16 ribs on the whorl between diameters of 80 and 170 mm. The inner ventrolateral and umbilical tubercles enlarge greatly at this stage. The umbilical tubercles are conical to bullate in shape and are consistently well developed. The ventrolaterals are rounded and conical at first, but later may become dorsoventrally expanded into wing-like structures. The umbilical and inner ventrolateral tubercles are joined by broad rounded ribs. There may be a siphonal depression between the opposing inner ventrolaterals or a flattened area may develop here. Occasionally, broad, vague, rib-like structures may be intercalated with the main ribs over the venter. The whorl sides are convexly rounded at this stage, the greatest breadth being just dorsal of the umbilical tubercle. As maximum size is approached the ribs become even more distant and the umbilical tubercles migrate towards the mid-flank region.

REMARKS. This material is readily comparable with *Acanthoceras amphibolum* Morrow, a common species in Texas (Stephenson 1952, Young & Powell 1978) and the western interior of the United States (Cobban & Scott 1972, Cobban 1977), which also occurs in Japan (Matsumoto *et al.* 1969) and probably in southern England (Matsumoto *et al.* 1969: 268). This species (see Morrow 1935, Hattin 1965, Cobban & Scott 1972, Cobban 1977) has a very similar ontogenetic development. In its early stages there is occasional multiplication of the siphonal tubercles and the outer ventrolaterals may be asymmetrically clavate. The siphonal tubercles fade, although a low keel may persist, and at adulthood there are massive inner ventrolateral and umbilical tubercles just as in the present specimens.

A series of hypernodose acanthoceratids occurs in the Middle Cenomanian of the western interior of the U.S.A. Of these, *Acanthoceras alvaradoense* Moreman (1942: 205; pl. 32, fig. 6; Stephenson 1955: 63; pl. 7, figs 1–9; Cobban 1977: 24; pl. 6, figs 1–7, 11–20) is very similar to *A. amphibolum* in its general ontogenetic development and adult morphology. According to Cobban (1977: 24), *A. alvaradoense* differs only in its earliest whorls, which bear constrictions at diameters of 10–12 mm, and in its less clavate outer ventrolateral and siphonal tubercles. There is no sign of constrictions in the Nigerian specimens and their siphonal and outer ventrolateral tubercles are normally markedly clavate. Another of these western interior forms is *'Plesiacanthoceras' wyomingense* (Reagan) (see Haas 1963, 1964). Again its adult morphology is close to that of the present material, although its umbilical tubercles do not appear to be so consistently well developed and its ventrolaterals may be highly spinose at this stage. In addition the outer ventrolateral tubercles appear to be even more clavate in the juvenile stages, while in the middle whorls there are twice as many ventrolateral as umbilical tubercles.

A Moroccan specimen described by Collignon (1966: 28; pl. 14; pl. 15, figs 1, 1a) as '*Euomphaloceras cornutum* (Kossmat)' does not seem to be conspecific with Kossmat's (1895: 11; pl. 5, figs 1a–c) *Acanthoceras cunningtoni* var. *cornuata* (itself a synonym of *Euomphaloceras cunningtoni cunningtoni* (Sharpe)). Instead its adult whorls resemble those in the present material but the details of its early stages are unknown.

Acanthoceras sp.

Fig. 42a, b

MATERIAL AND OCCURRENCE. A single specimen (C.83116) from the Odukpani Formation (Middle Cenomanian), 30·1 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83116	155	–	–	65 (42)
	86	34 (39·5)	32 (37)	33 (38)
	58	24 (41)	23 (39·6)	20 (34·5)

DESCRIPTION. This fully septate specimen has a diameter of 155 mm, and is evolute with more or less quadrate whorls.

In the earliest stages seen (between diameters of 15 and 20 mm) there are pointed inner ventrolateral tubercles each joined by an obliquely-directed swelling to a conical or clavate outer ventrolateral tubercle which is situated a little further adorally. There are low clavate siphonal tubercles tending to form an intermittent keel. There appear to be rather poorly developed umbilical tubercles at this stage corresponding to only some of the inner ventrolaterals. Low rounded ribs extend from the inner ventrolateral tubercles for a greater or lesser distance across the flanks. The umbilical tubercles are situated on the more persistent of these ribs. There are about nine rows of inner ventrolateral tubercles in each half whorl at this stage.

By a diameter of about 40 mm the umbilical tubercles are more prominent, as are the flank ribs. There are more inner ventrolateral than umbilical tubercles.

At diameters between about 55 and 85 mm there are 10 or 11 ribs per half whorl. They are narrow, high, rounded and unevenly spaced. Most bear a prominent, bullate, pointed umbilical tubercle but its strength varies and on every second to fifth rib it is markedly effaced. Each rib also bears a pair of inner ventrolateral tubercles, which are usually prominent and pointed but occasionally also weakly developed, joined by oblique swellings to corresponding conical or slightly clavate outer ventrolaterals. At this stage there are only faint, rounded, conical or clavate siphonal tubercles which are irregularly spaced and not always located exactly between the outer ventrolaterals. Occasional intercalated ventral ribs each bearing a low siphonal tubercle and a pair of weak outer ventrolaterals occur. They carry no inner ventrolateral tubercles but may pass onto the ventral part of the flank.

The remainder of the specimen is poorly preserved. In its last half whorl there are 12 narrow, rounded inequidistant ribs. The strength of the umbilical tubercles varies markedly. They may be so effaced as to be practically non-existent, but some are pronounced bullate structures: all intermediate strengths occur in no regular or consistent manner. The venter is unclear, but appears to be flattened. There is a ventrolateral horn on each rib but it seems to be only a low rounded cone.

The suture is rather finely subdivided with a deep E and a rather complex L.

REMARKS. In its early whorls this specimen is difficult to distinguish from the contemporary material of *Acanthoceras amphibolum* described above, agreeing in the occasional multiplication of the siphonal and outer ventrolateral tubercles and in the variable development of the umbilical tubercles. In the present individual, however, the latter character is exaggerated and persists into the adult stages, where the ribbing is denser and the ventrolateral tubercles weaker. This specimen does not conform closely to any other known species and probably represents a variant of *A. amphibolum*: the similarity of the two forms in their earlier stages seems to indicate a close relationship. Due to the paucity of the material at hand, however, the precise nature of this relationship and the appropriate taxonomic rank for this specimen are difficult to decide.

Subfamily **EUOMPHALOCERATINAE** Cooper, 1978

Genus ***EUOMPHALOCERAS*** Spath, 1923*a*

TYPE SPECIES. *Ammonites euomphalus* Sharpe, 1855; by the original designation of Spath, 1923*a*.

Euomphaloceras inerme (Pervinquière, 1907)

Fig. 44a, b

1826 *Ammonites rhotomagensis* J. de C. Sowerby: 25; pl. 515 (lower figure only).
1855 *Ammonites sussexiensis* Mantell; Sharpe: 34; pl. 15, figs 1a–d.
1907 *Acanthoceras cunningtoni* var. *inermis* Pervinquière: 277.
1923*a* *Acanthoceras sussexiense* (Mantell); Spath: 144.
1926 *Acanthoceras evolutum* Spath: 82.
1951 *Acanthoceras evolutum* Spath; Wright & Wright: 28.
1957 *Acanthoceras* aff. *evolutum* Spath; Matsumoto, Saito & Fukada: 33; pl. 14, fig. 2.
1971 *Euomphaloceras inerme* (Pervinquière) Kennedy: 94; pl. 59, figs 6a, 6b; pl. 61, figs 1a, 1b; pl. 62, figs 1a, 1b; pl. 64, fig. 1.

MATERIAL AND OCCURRENCE. Eleven specimens (C.82110, C.82141, C.82143, C.82147, C.83091, C.85264, UIN 477.1–5) from the Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar.

DESCRIPTION. The shell is evolute, reaching a diameter of some 300 mm. The whorl breadth is equal to, or a little greater than, the whorl height. The greatest intercostal breadth is at the level of the umbilical tubercles.

The earliest whorls are not seen. In the whorl up to a diameter of 70 mm there are about 18 major ribs. Each rib originates at a bullate umbilical tubercle and carries a pair of moderately spinose inner ventrolateral tubercles and pronounced clavate, rounded or pyramidal outer ventrolateral tubercles, and a more subdued, rounded or clavate siphonal tubercle. Alternating with the major ribs over the venter are one or more minor ribs which do not extend onto the whorl sides. The minor ribs carry a pair of outer ventrolateral tubercles, which are generally less pronounced than those of the major ribs and sometimes absent altogether, and a single siphonal tubercle of more or less equal strength to those of the major ribs.

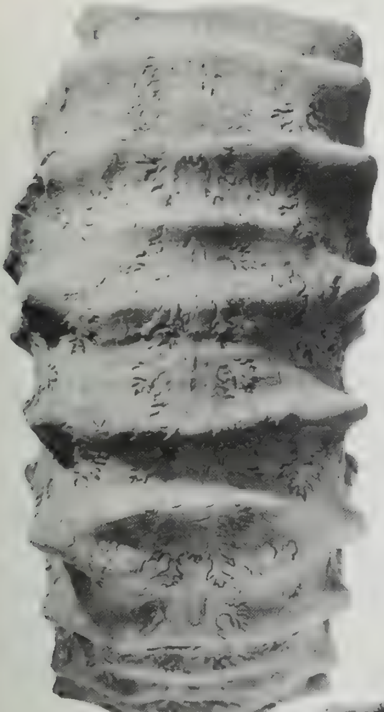
At diameters in excess of 70 mm the minor ribs tend to disappear, but persist in some individuals up to a diameter of over 100 mm. At these large diameters the minor ribs, when present, may be markedly convex. The major ribs increase in number to 20 or more in each whorl and are narrow, rounded and may be concave on the flanks. The umbilical, inner and outer ventrolateral tubercles appear only as swellings on the ribs. Along the siphonal line there may be a low swelling or a depression. At adulthood the inner and outer ventrolateral tubercles are difficult to distinguish as discrete swellings. The siphonal swellings tend to disappear, the ribs being uninterrupted over the venter or with a siphonal depression. The number of ribs decreases to 15 or 16 in each whorl at this stage.

The suture has a deep E, a highly subdivided bifid E/L and a highly subdivided L.

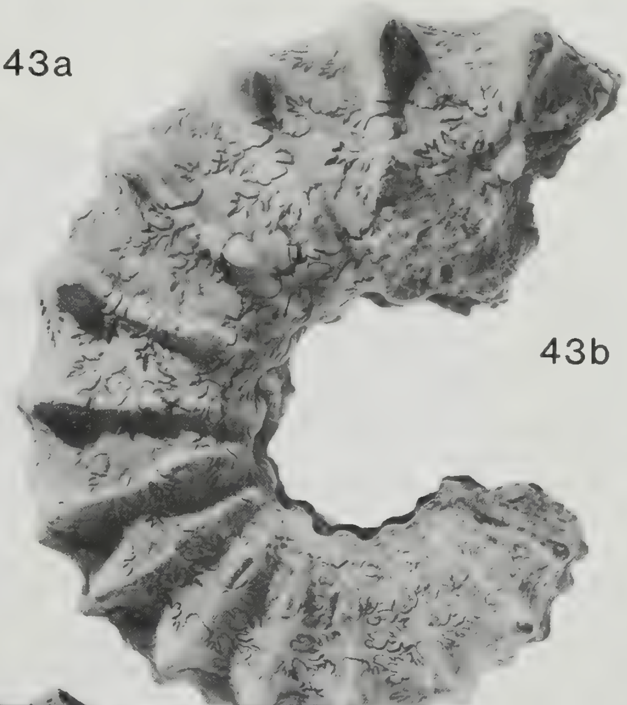
REMARKS. This material is most closely comparable with *Euomphaloceras inerme* (Pervinquière). The English material of this species, including the holotype, was described by Kennedy (1971: 94) and agrees in ontogenetic development and ornamentation with the Nigerian specimens. The development of the minor ribbing is variable in the Nigerian material, however, and densely ribbed variants may show a ventral ornament like that in *E. cunningtoni* (see pp. 42–51) although this species has markedly fewer major ribs. In other specimens the intercalated ribs are lost early in ontogeny, these individual coming to resemble the low Middle Cenomanian *Acanthoceras rhotomagense* var. *sussexiense* (Mantell 1822: 114; pl. 20, fig. 2; Kennedy & Hancock 1970: 472; pl. 89, fig. 2; pl. 91, figs 1, 2; pl. 92, figs 1, 2; text-figs 3, 4, 5, 6a). Specimens of this form transitional to *Euomphaloceras* also occur at Rouen, France (Kennedy & Hancock 1970: 474; pl. 92, fig. 4; pl. 93).

Fig. 43a, b *Euomphaloceras cunningtoni meridionale* (Stoliczka). Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar. C.82104, ×0·65. See also Figs 45, 46.

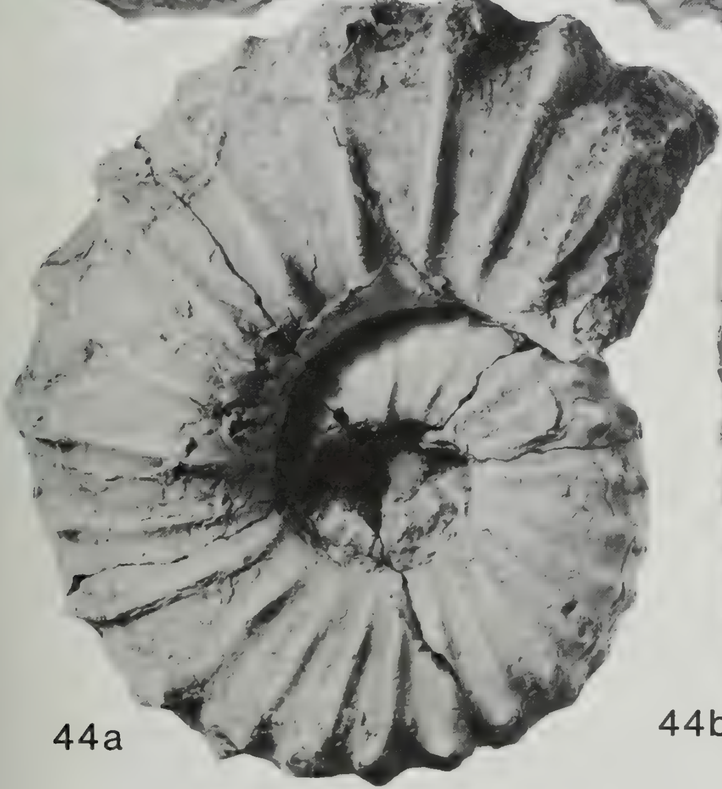
Fig. 44a, b *Euomphaloceras inerme* (Pervinquière). Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar. C.85264, ×0·75.



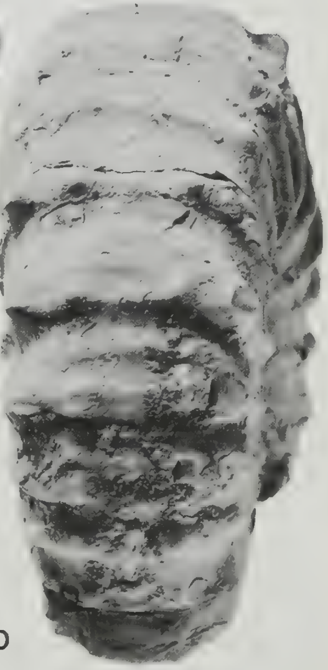
43a



43b



44a



44b

Euomphaloceras cunningtoni (Sharpe, 1855)

1855 *Ammonites cunningtoni* Sharpe: 35; pl. 15, figs 2a–c.
1863 *Ammonites cunningtoni* Sharpe; Pictet: 51; pl. 5, figs 2a–c (only).
1864 *Ammonites meridionalis* Stoliczka: 76; pl. 41, figs 1a–c.
1897 *Acanthoceras cunningtoni* var. *cornuata* Kossmat: 11; pl. 5, figs 1a–c.
? *non* 1904 *Acanthoceras cunningtoni* (Sharpe); Douvillé: 241; pl. 31, fig. 2.
1907 *Acanthoceras cunningtoni* (Sharpe); Pervinquière: 277; pl. 15, figs 1a–c.
1907 *Acanthoceras meridionale* (Stoliczka) Pervinquière: 278; pl. 15, figs 2–6.
1928 *Acanthoceras lonsdalei* Adkins: 244; pl. 26, fig. 5; pl. 27, fig. 3.
1933 *Acanthoceras cunningtoni* (Sharpe); Collignon: 63, figs 2, 3.
non 1940 *Acanthoceras meridionale* (Stoliczka) var. *multicostata* Basse: 446; pl. 6, figs 2a, 2b.
? 1940 *Cunningtoniceras cunningtoni* (Sharpe) Fabre: 234; pl. 8, fig. 5.
1944 *Cunningtoniceras höltkeri* Erni: 470; pl. 11.
1951 *Euomphaloceras euomphalum* (Sharpe); Wright & Wright: 29 (*pars*).
1952 *Acanthoceras*? *eulessanum* Stephenson: 201; pl. 47, fig. 5; pl. 48, figs 3, 4.
1955 *Euomphaloceras lonsdalei* (Adkins) Stephenson: 62; pl. 6, figs 6–20.
1957 *Euomphaloceras* cf. *euomphalum* (Sharpe); Matsumoto, Saito & Fukada: 34; pl. 15, fig. 3.
1963 *Euomphaloceras cunningtoni* (Sharpe) Wright: 607; pl. 88, fig. 2; pl. 89, fig. 1.
1963 *Euomphaloceras lonsdalei* (Adkins); Wright: 609; pl. 87, fig. 2; pl. 88, fig. 1; pl. 89, fig. 2.
1964 *Euomphaloceras euomphalum* var. *pervinquieri* Collignon: 145; pl. 373, fig. 1619.
? *non* 1966 *Euomphaloceras cornutum* (Kossmat); Collignon: 28; pl. 14; pl. 15, figs 1, 1a (?= *Acanthoceras amphibolum* Morrow).
1966 *Euomphaloceras pervinquieri* Collignon: 29.
1969 *Euomphaloceras meridionale* (Stoliczka); Matsumoto, Muramoto & Takahashi: 272; pl. 33, figs 1, 2; pl. 34, fig. 1; text-fig. 6.
1971 *Euomphaloceras cunningtoni* (Sharpe); Kennedy: 92; pl. 60, figs 1a, 1b; pl. 61, figs 2a, 2b.
1972 *Euomphaloceras* cf. *E. cunningtoni* (Sharpe); Cobban & Scott: 70; pl. 4, figs 4, 5; pl. 5, figs 6–8.
1972 *Euomphaloceras cunningtoni* (Sharpe); Thomel: 163; pl. 71, fig. 4; pl. 83; pl. 85, fig. 2; pl. 86, figs 1, 2; pl. 87, figs 1–6.
1972 *Euomphaloceras meridionale* (Stoliczka); Thomel: 165.
1973 *Euomphaloceras cunningtoni meridionale* (Stoliczka); Cooper: 61, figs 10A, 10B, 11, 12A, 12B, 13A.
? 1977 *Euomphaloceras* aff. *E. cunningtoni* (Sharpe); Cobban: 25; pl. 11, figs 17, 18.
1978 *Euomphaloceras cunningtoni* (Sharpe); Wiedmann & Kauffman: pl. 5, fig. 5.
1978 *Euomphaloceras lonsdalei* (Adkins); Young & Powell: pl. 5, figs 1, 7.
1978*a* *Euomphaloceras cunningtoni meridionale* (Stoliczka); Cooper: 6, fig. 8.

REMARKS. Members of the *Euomphaloceras cunningtoni* group are significant elements of Middle Cenomanian faunas. They have a virtually global distribution occurring in Europe, the Middle East, north and west Africa, the Malagasy Republic, India, Australasia, Japan and the United States. Their ornamentation varies widely and this, coupled with the lack of large population samples, has led to much debate concerning their precise relationships and distinguishing characters. The two main representatives, *E. cunningtoni* (Sharpe) and *E. meridionale* (Stoliczka), were considered by Matsumoto *et al.* (1969) and Thomel (1972) to be distinct species. Matsumoto *et al.* (1969: 275) distinguished *E. meridionale* on the basis of its more obvious multiplication of the ribs over the venter, each rib bearing a siphonal and a pair of outer ventrolateral tubercles; the bifurcation of the ribs at the inner ventrolateral tubercles; the predominantly lateral extension of the last-mentioned tubercles; and by its broad whorls. Thomel (1972: 165) also stressed the multiplication of both the siphonal and the outer ventrolateral tubercles in *E. meridionale* but considered its adult morphology to be distinctive as well, there being prominent horns while *E. cunningtoni* displays ribs without prominent tubercles at large diameters. Wright (1963: 608) has also remarked upon the differences in ventral ornamentation, but considered them to warrant only subspecific separation, a conclusion adopted by Kennedy (1971: 93). One of the main problems in this group is the relatively meagre amount of material. The recovery, from a single horizon in the Odukpani Formation, of the 99 specimens referred to *E. cunningtoni cunningtoni* (Sharpe), below, allows improved understanding of individual variation. These specimens show considerable inconsistency in their ornamental details and although the population is centred on a morphology close to *E. cunningtoni* many individuals are of a decidedly *E. meridionale* character. Another smaller collection, from a horizon some 30–35 m below the first, contains individuals of a more consistently *E. meridionale* type. The youngest material of this group in the Odukpani Formation represents a new form described here and assigned to *E. cunningtoni alatum* subsp. nov. These three forms seem to represent stratigraphically successive subspecies whose mean population structure is slightly different but which show considerable overlap between the end members. Such a situation was suspected by Kennedy & Hancock (1977: 135). Younger forms in the Odukpani Formation display a lesser tendency towards multiplication of the ventral ribbing and tuberculation, but in their adult stages show increasingly pronounced ventrolateral ornament.

In Texas and the western interior of the United States the *E. cunningtoni* group is most commonly represented by *E. lonsdalei* (Adkins 1928: 244; pl. 26, fig. 5; pl. 27, fig. 3; Stephenson 1955: 62; pl. 6, figs 6–20). *E. lonsdalei* is close to *E. cunningtoni cunningtoni* but differs in its less depressed whorl section, rather denser major ribbing and reduced multiplication of the ventral ribs and tubercles. Variation within the present Nigerian material indicates that *E. lonsdalei* does not deserve separation at the species level but is best regarded as another subspecies of *E. cunningtoni* (see also Kennedy 1971: 93–94). In Texas Stephenson (1955: 201) reported *E. cunningtoni lonsdalei* in beds a little above those containing *Acanthoceras eulessanum* Stephenson, a synonym of *E. cunningtoni cunningtoni.* A similar sequence occurs in Colorado (Cobban & Scott 1972: pl. 40). Here, forms close to *E. cunningtoni cunningtoni* occur in the lower part of the Middle Cenomanian, while *E. cunningtoni lonsdalei* characterizes higher beds in the Zone of *Acanthoceras muldoonense.*

It appears, therefore, that changes in ornamental details in this group are the result of age differences. Since individual variation may be important, however, accurate diagnosis of members of the group may require large population samples. For this reason no comprehensive attempt is made here to assign those previously described specimens to a particular subspecies. Reasonably secure determinations are, nevertheless, indicated below.

Euomphaloceras cunningtoni meridionale (Stoliczka, 1864)

Figs 43, 45, 46

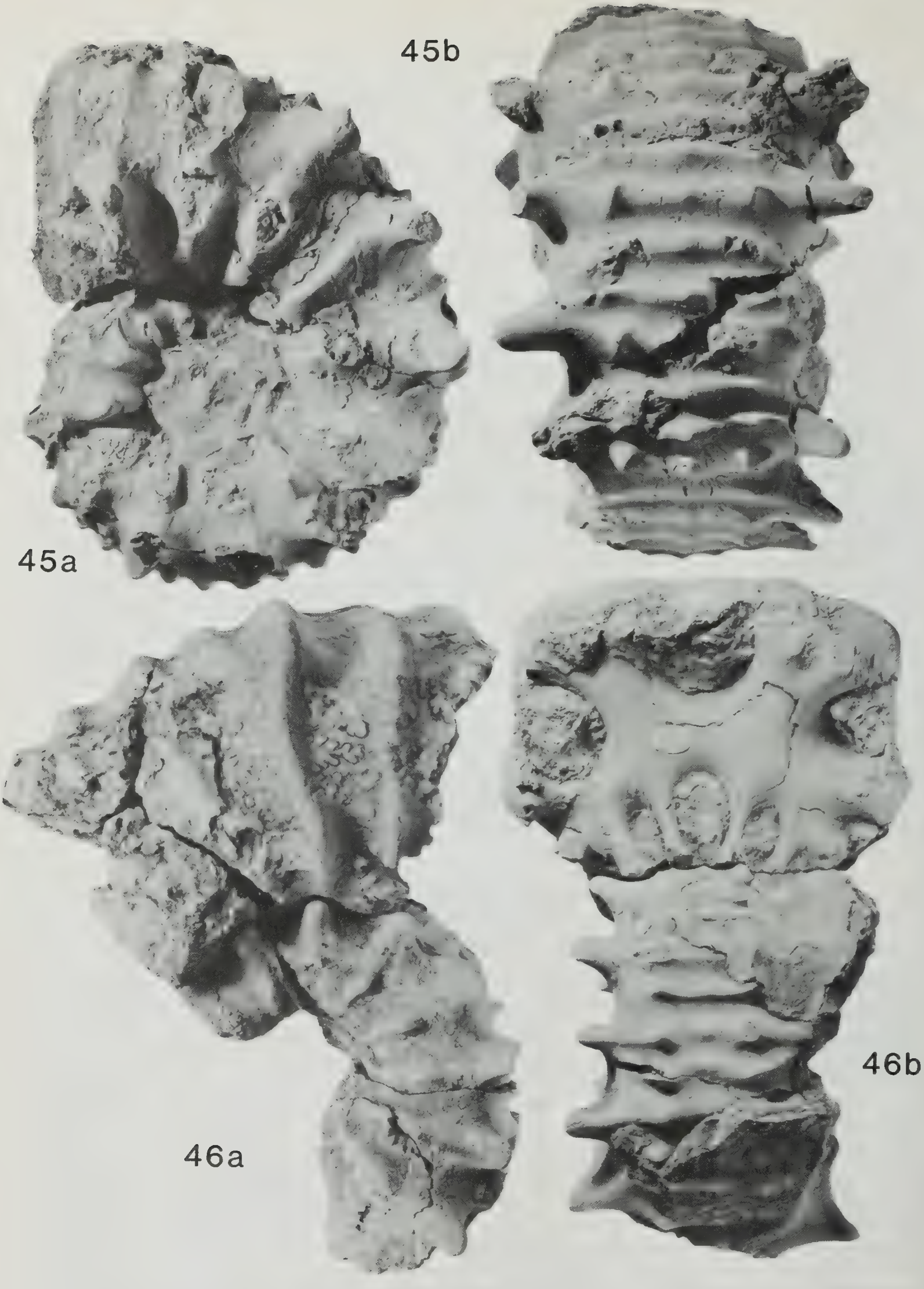
1864 *Ammonites meridionalis* Stoliczka: 76; pl. 41, figs 1a–c.

MATERIAL AND OCCURRENCE. Eight specimens (C.82104, C.82139, C.82142, C.83092, UIN 478.1–4) from the Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83092	165	90 (54·5)	68 (41)	61 (37)

DESCRIPTION. The shell is evolute, reaching a diameter of over 230 mm. The whorls are broader than high, the greatest intercostal breadth being at the level of the umbilical tubercles.

In C.82139 there are 12 or 13 major ribs in the complete whorl between diameters of 35 and 90 mm; their frequency increases during ontogeny. In the middle growth stages in C.83092 there are 16 or 17 in each whorl. On the flank each major rib generally bears a prominent, bullate pointed umbilical tubercle, although this may occasionally be effaced, and a long, usually spinose inner ventrolateral tubercle extended chiefly in a lateral direction. Over the venter the major ribs normally bifurcate at the inner ventrolateral tubercles and a further minor rib is usually intercalated with these looped pairs of ribs. Over the venter each rib bears a pair of prominent rounded outer ventrolateral tubercles and a



Figs 45, 46 *Euomphaloceras cunningtoni meridionale* (Stoliczka). Odukpani Formation (Middle Cenomanian), 27·9 km from Calabar. Fig. 45a, b, C.82139, ×1. Fig. 46a, b, C.83092, ×0·65. See also Fig. 43.

more subdued siphonal tubercle which becomes decreasingly conspicuous as growth proceeds. The outer ventrolaterals immediately adjacent to the inner ventrolateral tubercles may be especially prominent. In one specimen (UIN 478.3) the outer ventrolateral tubercles are markedly clavate in places and each corresponds to two siphonal tubercles.

At diameters in excess of 150 mm neither the umbilical nor the inner ventrolateral tubercles develop into horns or spines. The ornament here consists of narrow, rounded ribs, often concave on the flanks, upon which the umbilical, inner and outer ventrolateral tubercles manifest themselves as bullate rounded swellings. In the siphonal region there may be a faint swelling or a depression on the ribs, or they may be broadly arched. An occasional rib runs obliquely across the venter, not meeting its fellow on the opposite side but terminating before reaching the ventrolateral shoulder. At these large diameters there are still some minor ribs alternating with the major ribs over the venter. They may be broadly arched structures or show swellings at the level of the outer ventrolateral tubercles and, less commonly, along the siphonal line. There appear to be more than 20 major ribs in each whorl at this stage.

The suture is fairly complex with E deep, E/L large, bifid and florid and L broad, deep and highly subdivided.

REMARKS. This population conforms closely with *Euomphaloceras cunningtoni meridionale* (Stoliczka 1864: 76; pl. 41, figs 1a–c) in gross morphology, ornament, suture pattern and in the persistence of minor intercalated ribs at large diameters. In the Nigerian material, tubercle development is suppressed during the later growth stages although Stoliczka (1864: 76) mentioned long, thick ventrolateral spines in his large specimens. A similar variation in adult ornamentation exists between material of *E. cunningtoni cunningtoni* described by Thomel (1972) and that dealt with below.

The differences between the material referred here to *E. cunningtoni meridionale* and that to *E. cunningtoni cunningtoni* are largely a matter of overall population structure. *E. cunningtoni meridionale* is characterized by the generally equal multiplication of its siphonal and outer ventrolateral tubercles, by the bifurcation of the major ribs over the venter, by its more persistent minor ribs and by not showing amalgamation of the inner and outer ventrolateral tubercles at large diameters.

Apart from the lectotype (see Stoliczka 1864: pl. 41, figs 1a–c), little of the previously described material can be confidently assigned to this subspecies, but specimens figured by Matsumoto *et al.* (1969: pl. 33, figs 1, 2; pl. 34, fig. 1) may well belong here.

***Euomphaloceras cunningtoni cunningtoni* (Sharpe, 1855)**
Figs 47–52

1855 *Ammonites cunningtoni* Sharpe: 35; pl. 15, figs 2a–c.

MATERIAL AND OCCURRENCE. Ninety-nine specimens (C.83097–102, C.83431–66, UIN 422.1–57) from the Odukpani Formation (Middle Cenomanian), 28·3 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83431	110	41 (37)	39 (35·5)	42 (38)
C.83097	100	37 (37)	36 (36)	40 (40)
C.83099	91	41 (45)	35 (38·5)	33 (36)
C.83100	85	28 (33)	31 (36·5)	32 (37·7)
C.83434	65	28 (42·4)	27 (41)	20 (30·7)

DESCRIPTION. The shell is evolute, the umbilicus widening during ontogeny. Whorl breadth may be distinctly greater than its height or the whorls may be higher than broad. The venter and the flanks are flattened in the early stages but tend to become rounded later on. The largest of the present specimens has a diameter of some 150 mm.

In the middle growth stages the ornamental details are highly variable. In each whorl there are about 12 major ribs which are rounded and narrower than the interspaces. On the flank,

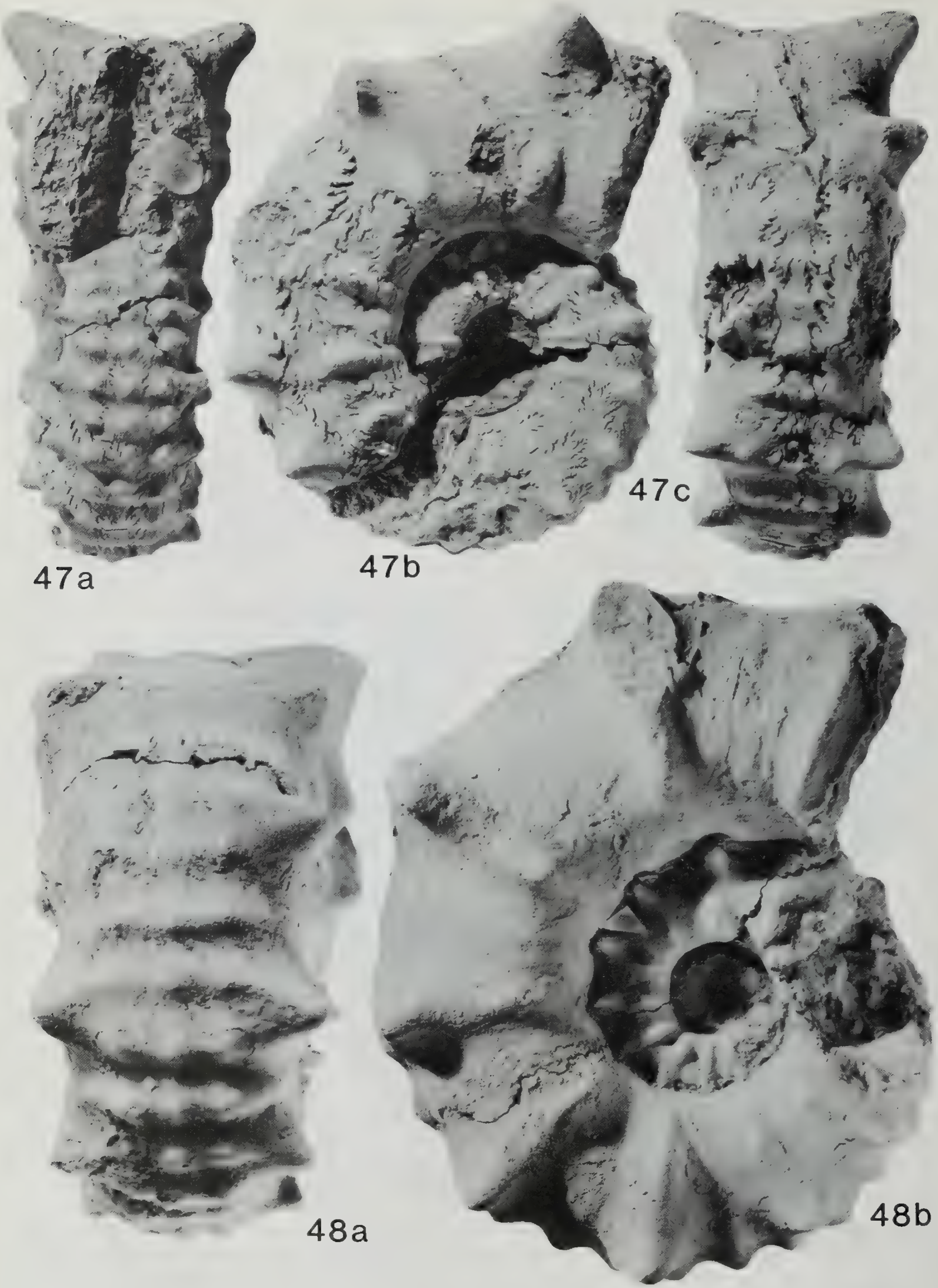
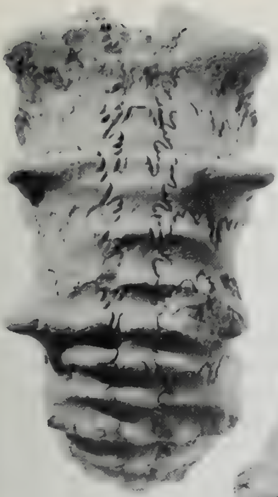


Fig. 47, 48 *Euomphaloceras cunningtoni cunningtoni* (Sharpe). Odukpani Formation (Middle Cenomanian), 28·3 km from Calabar. Fig. 47a–c, C.83100, ×1. Fig. 48a, b, C.83431, ×1. See also Figs 49–52.



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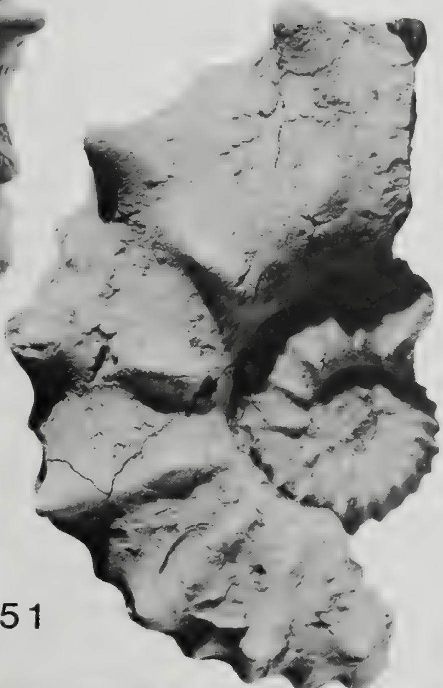

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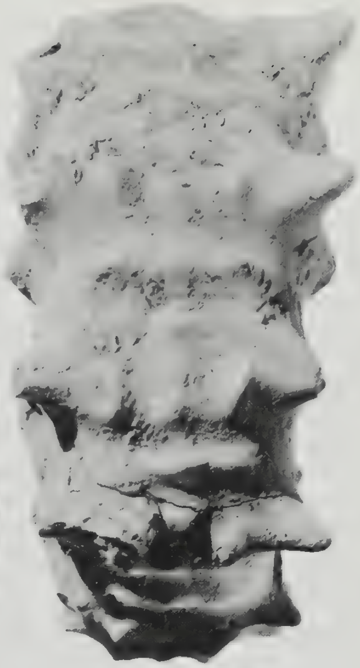

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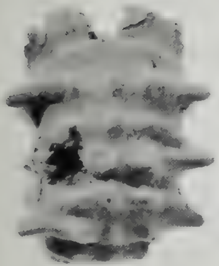

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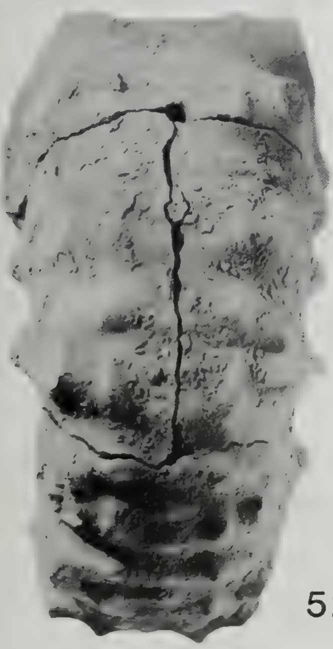

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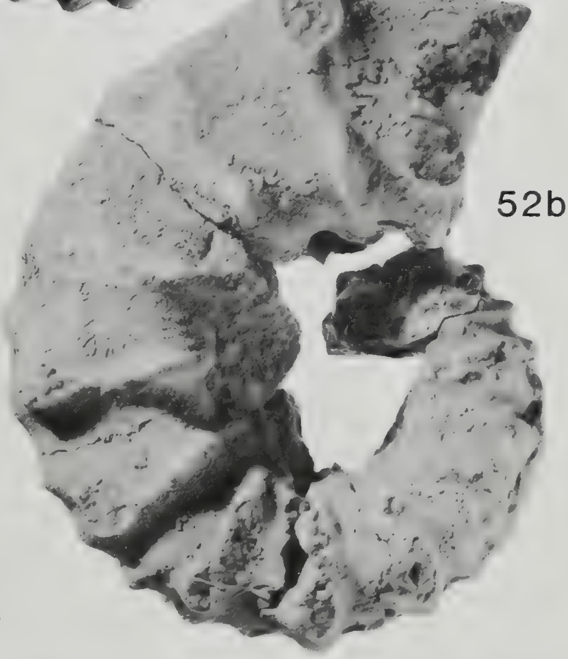


52b

Figs 49–52 *Euomphaloceras cunningtoni cunningtoni* (Sharpe). Odukpani Formation (Middle Cenomanian), 28·3 km from Calabar. Fig. 49, C.83440, ×1. Fig. 50a, b, C.83099, ×1. Fig. 51, C.83444, ×1. Fig. 52a, b, C83437, ×1. See also Figs 47, 48.

each rib carries a bullate, rounded umbilical tubercle and a pointed inner ventrolateral tubercle which predominantly extends laterally or ventrolaterally and becomes increasingly prominent as growth proceeds. The major ribs may pass transversely over the venter, or bifurcate in a more or less obvious manner. This usually occurs at the inner ventrolateral tubercles, but sometimes at the outer ventrolaterals. Each of these ventral ribs normally carries a pair of variably pronounced outer ventrolateral tubercles (except when bifurcation occurs here) and a rounded or clavate siphonal tubercle. There are often intercalated minor ventral ribs present as well, each of which may bear a siphonal and a pair of outer ventrolateral tubercles, although frequently the siphonal tubercle occurs in isolation or with only low indefinite outer ventrolateral tubercles. In rare cases, these intercalated ribs also include a pair of low inner ventrolateral tubercles. Asymmetry is common owing to the displacement of siphonal tubercles from the mid-line or to the absence or displacement of one of the inner or outer ventrolateral tubercles. In some individuals there is a regular alternation of a non-bifurcating major rib and a single minor rib. In others there are bifurcating major ribs alternating with one or two minor ribs or isolated siphonal tubercles. Consequently, there are two to four siphonal tubercles to each pair of inner ventrolaterals. The outer ventrolateral tubercles may be rounded or markedly clavate. In the latter cases each corresponds to two siphonal tubercles. The minor ribs may be transverse or convexly curved.

Minor ribs rarely occur at diameters in excess of 60 to 80 mm. When persistent, they tend to be markedly convex or appear only as a siphonal swelling. The tendency towards bifurcation of the major ribs over the venter decreases at this stage. The inner and outer ventrolateral tubercles fuse at large diameters, usually forming a bituberculate horn. There is, normally, a siphonal depression between the horns although they may fuse across the venter. The horns vary in shape, extending predominantly laterally or ventrolaterally and sometimes enlarging dorsally to absorb the umbilical tubercle, so forming a wing-like structure. In large specimens asymmetry is again common owing to abnormalities in the ornament. Often one of a pair of ventrolateral horns is absent or displaced, its associated rib running obliquely across the venter and dying out before reaching the opposite ventrolateral shoulder.

The suture is fairly simple with a moderately deep E, a large bifid E/L and a fairly narrow simple L.

REMARKS. Although this population is highly variable, its mean structure is closest to that in *Euomphaloceras cunningtoni cunningtoni* (Sharpe), the holotype of which was redescribed and figured by Kennedy (1971: 92; pl. 60). In particular, siphonal tubercles outnumber both inner and outer ventrolaterals and large bituberculate horns develop towards adulthood. In the holotype the outer ventrolateral tubercles are markedly clavate, each corresponding to two siphonal tubercles. Many of the present specimens show this pattern, either consistently or in places. It is, however, by no means universal amongst the population as a whole. The present material indicates that Wright (1963: 608) was correct in allowing little weight to minor details of the ventral ornamentation in the *E. cunningtoni* group. Certain individuals in this collection could be placed with some confidence in *E. cunningtoni meridionale* if found alone, showing that overall population structure is a matter of importance here.

In their adult stages the Nigerian specimens commonly display large bituberculate horns, as do the holotype of *E. cunningtoni cunningtoni* and other large individuals (see, for example, Kossmat 1897: pl. 5, figs 1a–c; Kennedy 1971: pl. 61, fig. 2). Thomel (1972: 163), however, described specimens from southern France in which bituberculate horns give way, at diameters in excess of 150 mm or so, to a ribbed ornament with only feeble swellings at the level of the ventrolateral tubercles. A similar adult ornament exists in the Nigerian material referred to *E. cunningtoni meridionale*, above. The question arises, is this a normal ornament for adults in the *E. cunningtoni* group, or is there some variation in this feature, stratigraphic or otherwise? As far as the Nigerian material is concerned, the earliest member of the group (*E. cunningtoni meridionale*) lacks prominent tubercles in the adult while the later members (*E. cunningtoni cunningtoni* and *E. cunningtoni alatum*) show increasingly massive ventrolateral horns, suggesting that changes in these features are correlated with stratigraphical age differences.

Amongst the present specimens are individuals with whorls higher than broad and others with a predominantly one to one alternation of major and minor ribs. In these respects they resemble *E. lonsdalei* (Adkins 1928, Stephenson 1955, Wright 1963). This morphological overlap demonstrates that, as mentioned above, *E. lonsdalei* is best considered as a subspecies of *E. cunningtoni*.

The difficulties involved in the determination of members of this group have been mentioned above. The majority of previously described specimens, however, appear to fall within the range of *E. cunningtoni cunningtoni* as it is conceived here. Apart from the holotype, the specimens figured by Pictet (1863: pl. 5, figs 2a–c), Kossmat (1897: pl. 5, figs 1a–c), Pervinquière (1907: pl. 15, figs 1a–c), Erni (1944: pl. 11), Stephenson (1952: pl. 47, fig. 5; pl. 48, figs 3, 4), Wright (1963: pl. 88, fig. 2; pl. 89, fig. 1), Kennedy (1971: pl. 61, figs 2a, 2b) and Wiedmann & Kauffman (1978: pl. 5, fig. 5) all seem to belong here. Specimens from Angola described by Cooper (1973: 61; figs 10A, 10B, 11, 12A, 12B, 13A; 1978*a*: fig. 8) as *E. cunningtoni meridionale* sometimes show isolated siphonal tubercles and in this respect appear closer to the Nigerian material of *E. cunningtoni cunningtoni*.

Euomphaloceras cunningtoni alatum subsp. nov.
Figs 53–56

HOLOTYPE. C.83479, portions of an adult and a middle whorl (Fig. 53a–c) from the Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar.

PARATYPES. Sixteen specimens (C.83108–12, C.83480–5, UIN 485.1–5), all from the same locality as the holotype.

OTHER MATERIAL. Two further specimens (C.85247, UIN 486.1) from the Odukpani Formation (Middle Cenomanian), 32·2 km from Calabar probably also belong here.

NAME. From the wing-like horns developed in adults.

DIAGNOSIS. *Euomphaloceras* of the *E. cunningtoni* group, distinguished by the typical intercalation of a single minor rib with each major rib in the early and middle stages and by the development of massive wing-like extensions enveloping the whorl sides and outer part of the venter in the adult.

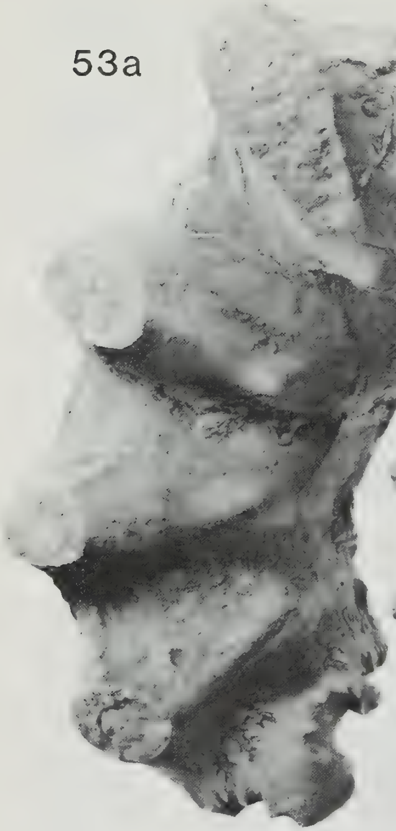
DIMENSIONS.	D	Wb	Wh	U
C.83484	80	44 (55)	35 (44)	31 (39)
C.83108	70	36 (51·4)	–	27 (38·6)

DESCRIPTION. The shell is evolute, the whorls usually being distinctly broader than high with the flanks and the venter rather flattened. The maximum diameter attained is about 200 mm.

Up to a diameter of about 10 mm the flanks are smooth. At this point narrow, rounded, unevenly-developed prorsiradiate ribs appear carrying uneven, often highly effaced umbilical tubercles and more pronounced inner ventrolateral tubercles. The venter is not seen at this stage. By a diameter of 25 mm, the ribs are rectiradiate with definite umbilical tubercles; even at this early stage the inner ventrolateral tubercles are decidedly spinose, the dorsum of the succeeding whorl being notched for their reception. Each major rib also bears a pair of rounded to clavate outer ventrolateral tubercles and a siphonal tubercle. Alternating with each major rib over the venter is a single, short, ventral rib carrying identical outer ventrolateral and siphonal tubercles. At first, however, this alternation of major and minor ribs is not so regular.

Between diameters of 30 and 80 mm there are approximately 13 major ribs in each whorl. They are narrow and rounded, bearing on the flank a prominent bullate umbilical tubercle centred a little outside the umbilical shoulder, and a highly spinose inner ventrolateral

53a



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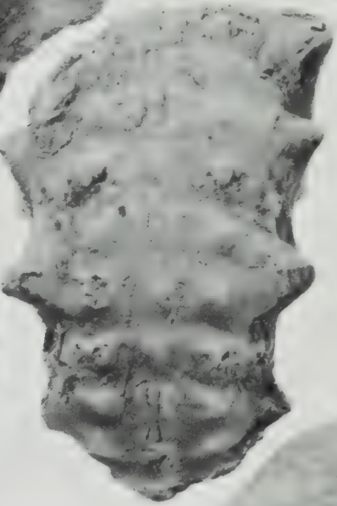

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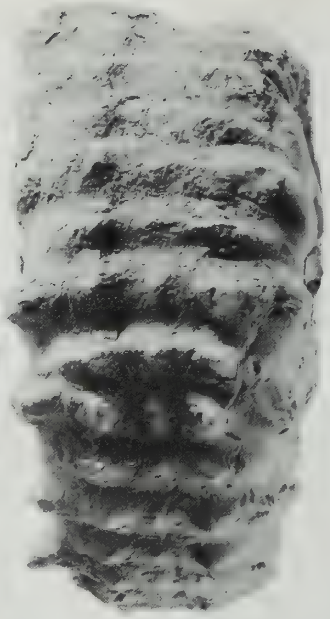

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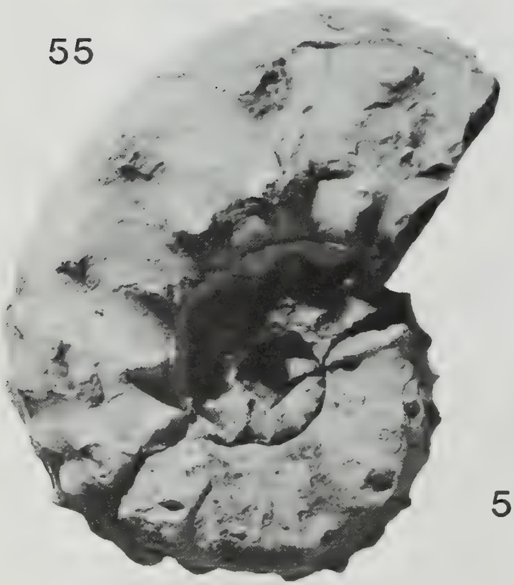

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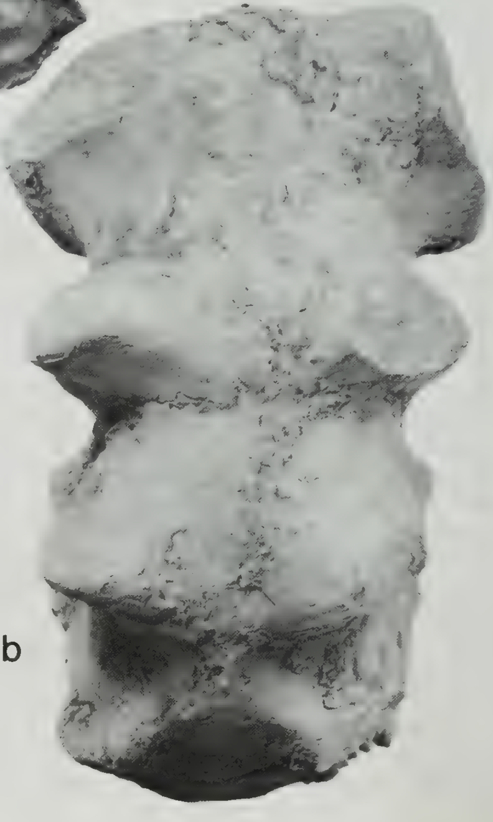


tubercle. The ribs continue over the venter where they may be transverse or slightly convex. Here each carries a pair of prominent, rounded, conical or clavate outer ventrolateral tubercles and a weaker rounded siphonal tubercle. As growth proceeds the siphonal tubercle becomes progressively weaker. In six (C.83108, C.83481–4, UIN 485.1) of the seven specimens in which this feature is displayed, a single minor rib alternates with each major rib over the venter. In the remaining specimen, the holotype (C.83479), the major ribs bifurcate over the venter and there may be a further rib intercalated with these pairs. Each minor rib carries a pair of outer ventrolateral and a siphonal tubercle developed to exactly the same degree as those of the major ribs. The ventral ribs are commonly convexly curved.

At diameters in excess of 80 mm, the outer ventrolateral and siphonal tubercles and the minor ribs become progressively weaker and, by a whorl height of some 50 mm (diameter approximately 125 mm) they are barely noticeable. At this stage the umbilical tubercles are enlarged and joined to the inner ventrolaterals by broad, rounded ribs. The inner ventrolateral tubercles now become enlarged into horn-like structures. As growth proceeds to full size, all trace of the minor ribs disappears. The ventrolateral horns continue to enlarge, at first assuming a pyramidal shape and finally becoming expanded into narrow wing-like structures enveloping the whorl sides and absorbing the umbilical tubercles. They extend onto the outer part of the venter but there is usually a siphonal depression centrally. The 'wings' may be roughly triangular or pentagonal in shape, extending predominantly laterally or ventrolaterally.

The suture has a deep E, a large deeply bifid E/L and a deep L divided by two elements in the middle stages, but in the adult the suture may be much simplified, L being shallow and broad.

Remarks. Certain adults in the Nigerian population of *E. cunningtoni cunningtoni*, described above, develop an ornament rather similar to that of *E. cunningtoni alatum* with wing-like ventrolateral extensions, but this character is more pronounced and consistent in the latter subspecies. These two forms also overlap in the details of their ventral ribbing in the early and middle stages; mean population structure is, however, quite different, *E. cunningtoni alatum* only rarely showing more than a single extra ventral rib. As mentioned above these differences seem to be age-related.

E. asura Matsumoto & Muramoto (Matsumoto *et al.* 1969: 277; pl. 35, fig. 1; pl. 36, fig. 1), which according to Kennedy & Hancock (1977: 136) is a junior synonym of *E. multicostatum* (Basse 1940: 446), also develops prominent adult ventrolateral tubercles, but these are much more spinose than in the present material. *E. lehmanni* Collignon (1966: 28; pl. 13, fig. 1) shows a regular alternation of long and short ribs in its middle stages – the adult is unknown – and may be closely related to *E. cunningtoni alatum*. It is, however, rather more densely ribbed. Certain of the horned acanthoceratids of the western interior of the U.S.A. develop a wing-like ornament, for example *Acanthoceras amphibolum* Morrow and *A. muldoonense* Cobban & Scott (see Cobban & Scott 1972), but their early and middle stages are quite different and they are not closely related to the present material.

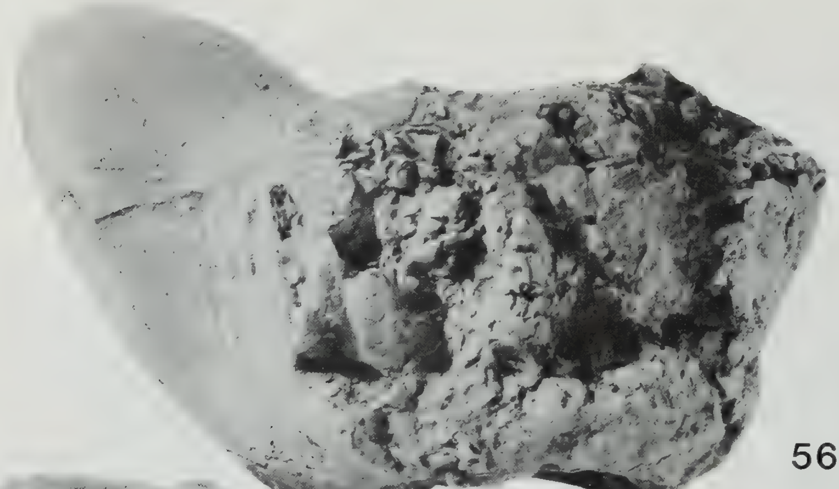
Genus ***KAMERUNOCERAS*** Reyment, 1954*a*

Type species. *Acanthoceras eschii* Solger, 1904; by the original designation of Reyment, 1954*a*.

Kamerunoceras tinrhertense Collignon, 1965
Figs 57–59

1965 *Kamerunoceras tinrhertense* Collignon: 175; pl. D.

Figs 53–55 *Euomphaloceras cunningtoni alatum* subsp. nov. Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar. Fig. 53a–c, **holotype** C.83479: Fig. 53a, b show outer whorls ×0·65, Fig. 53c shows ventral view of the preceeding whorl ×1. Fig. 54, paratype C.83108 in ventral view, ×1. Fig. 55, paratype C.83484, ×1. See also Fig. 56.



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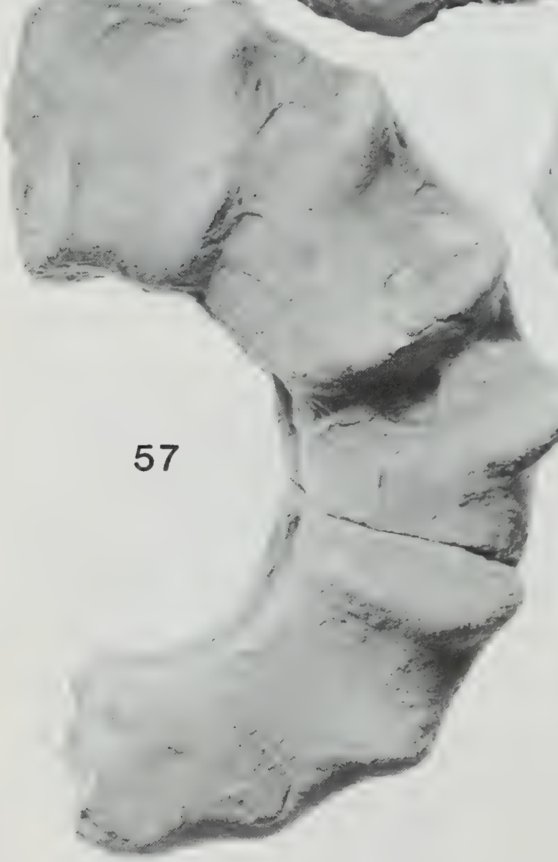

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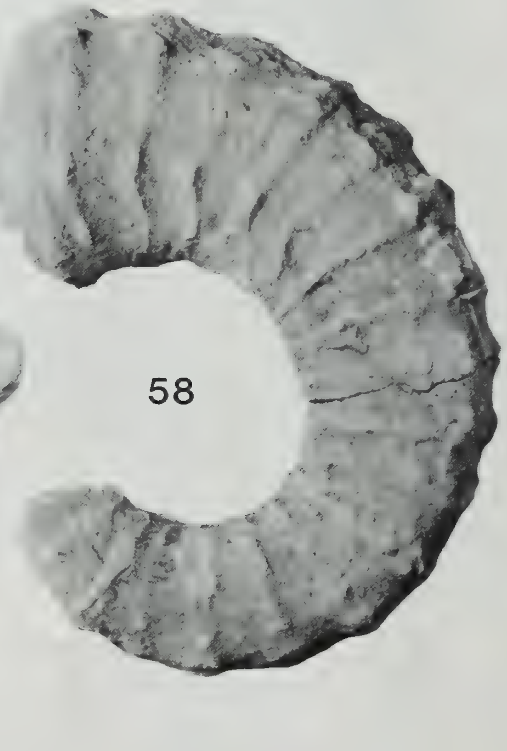

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Fig. 56 *Euomphaloceras cunningtoni alatum* subsp. nov. Odukpani Formation (Middle Cenomanian), 30·3 km from Calabar. Paratype C.83111, ×1, apertural view showing adult ventrolateral ornament. See also Figs 53–55.

Figs 57, 58 *Kamerunoceras tinrhertense* Collignon. Odukpani Formation (Lower Turonian), 34 km from Calabar. Fig. 57, C.83489, ×0·65. Fig. 58, C.83493, ×0·75. See also Fig. 59.

MATERIAL AND OCCURRENCE. Twenty-one specimens (C.83126–7, C.83489–94, UIN 426.1–13) from the Odukpani Formation (Lower Turonian), 34 km from Calabar.

DESCRIPTION. The shell is very evolute and reaches a diameter of at least 200 mm. The whorls are rectangular being slightly to distinctly higher than broad.

The earliest whorls are not seen. Between diameters of about 70 and 110 mm there is considerable variation in ornamentation, the number of ribs varying between extremes of 24 and about 40 to a whorl. Most ribs are long and narrow, each with a rounded to bullate umbilical tubercle and a pair of inner and outer ventrolateral tubercles. There are also clavate siphonal tubercles tending to form an intermittent keel. On some of the ribs the umbilical tubercles are markedly effaced and often absent altogether, these ribs being confined to the ventral part of the flank. In some specimens there is a fairly regular alternation of long and short ribs. The umbilical tubercles tend to migrate ventrally towards the mid-flank region during ontogeny and often a further tubercle develops on the umbilical shoulder. The ribs may be prorsiradiate between these pairs of umbilical tubercles and somewhat rursiradiate to rectiradiate on the ventral part of the flank.

As growth proceeds, the siphonal and outer ventrolateral tubercles fade and finally disappear while the inner ventrolaterals enlarge markedly. The umbilical tubercles swell into large bullate structures occupying the whole of the dorsal half of the whorl sides. The ribs become broader and more widely spaced at large diameters. In the adult whorl there are only 14–15 ventrolateral tubercles and fewer umbilical tubercles. In some cases each umbilical tubercle may correspond in a regular fashion to two ventrolaterals, while in others the umbilical tubercles are more numerous but sporadically distributed. At adulthood the ventrolateral tubercles may tend to fuse across the venter.

The suture is simple with a narrow E, a broad bifid E/L, a rather narrow L, a simple asymmetrically bifid L/U_2 and a narrow shallow U_2.

REMARKS. *Kamerunoceras tinrhertense* Collignon (1965: 175; pl. D) is based upon a single wind-worn specimen from the Lower Turonian of the Algerian Sahara, and knowledge of its morphology and individual variation is therefore incomplete. It is clear, however, that the present material agrees with this species in important aspects of its morphology and ontogeny as well as in its large size. In particular the ribbing is dense in the early stages, while at adulthood there are coarsely ornamented, distant ribs. Ventrolateral tubercles outnumber umbilicals throughout middle and late ontogeny.

In their middle growth stages the present specimens may show approximately the same rib density as *K. turoniense* (d'Orbigny) and those variants with few intercalated ribs rather resemble that species at this stage (see Fig. 58; Kennedy & Wright 1979: pl. 3, fig. 1). In addition both show duplication of the umbilical tubercles (see above; Pervinquière 1907: pl. 19, fig. A; Kennedy & Wright 1979: 1174). *K. turoniense*, however, has more distant ribs in its early stages, dense weaker ribbing in the adult, and also lacks intercalated ribs.

Rather similar to the present material in general shape and suture pattern, and in showing long and short ribs with duplication of the umbilical tubercles, is *Polyaspidoceras shimizui* Matsumoto (Matsumoto, Kawashita, Fujishima & Miyauchi 1978: 21, fig. 7). This form, however, possesses yet another extra row of tubercles on the flank. This species was made the basis of the new genus *Polyaspidoceras* but it is questionable whether it is separable from *Kamerunoceras*.

Probably conspecific with the present material are specimens collected in the Odukpani Formation a little to the east of the present road section and referred by Fayose (1977: 237, fig. 4) to *Hoplitoides crassicostatus* Reyment.

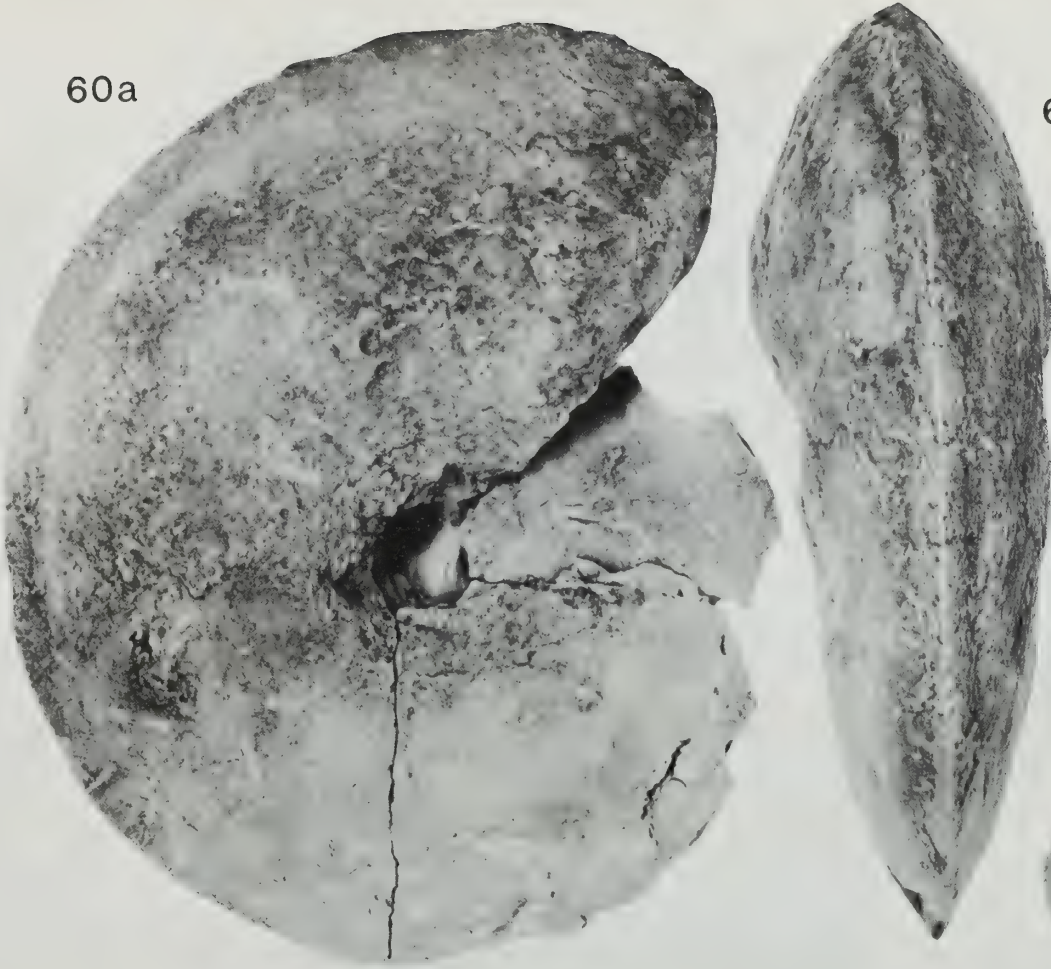
Family **COILOPOCERATIDAE** Hyatt, 1903

Genus ***COILOPOCERAS*** Hyatt, 1903

TYPE SPECIES. *Coilopoceras colleti* Hyatt, 1903; by original designation.

60a

60b



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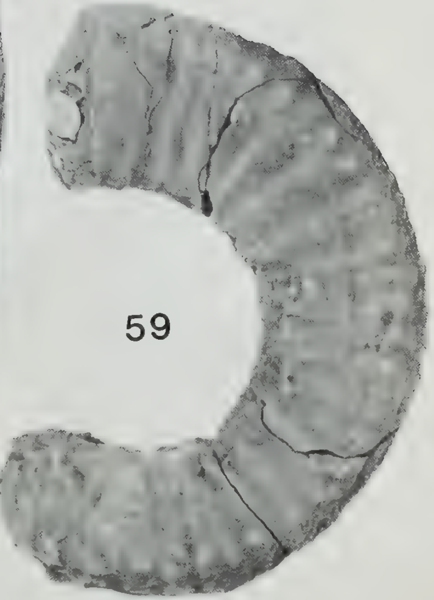


Fig. 59 *Kamerunoceras tinrhertense* Collignon. Odukpani Formation (Lower Turonian), 34 km from Calabar. C.83494, ×0·75. See also Figs 57, 58.

Fig. 60a, b *Coilopoceras* aff. *newelli* Benavides-Cáceres. Odukpani Formation (Lower Turonian), 34 km from Calabar. C.83486, ×0·65, a specimen showing average whorl breadth and strength of ornamentation. See also Figs 61, 62.

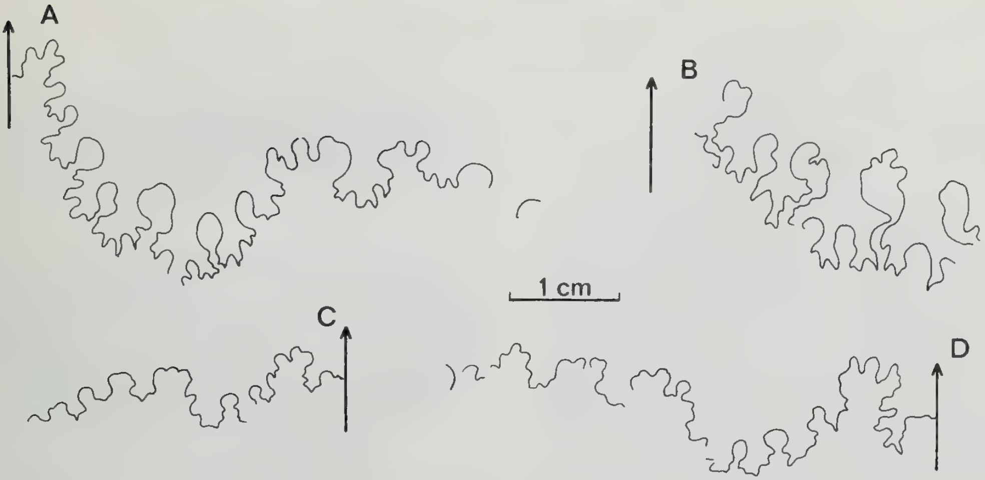


Fig. 61 Sutures in *Coilopoceras* aff. *newelli* Benavides-Cáceres. A, C.83123 at whorl height of 90 mm; B, UIN 427.3; C, C.83124 at whorl height of 60 mm; D, UIN 427.4 at whorl height of 90 mm.

Coilopoceras aff. *newelli* Benavides-Cáceres, 1956
Figs 60–62

Compare: 1956 *Coilopoceras newelli* Benavides-Cáceres: 473; pl. 61, figs 4, 5; pl. 62, figs 5–7.

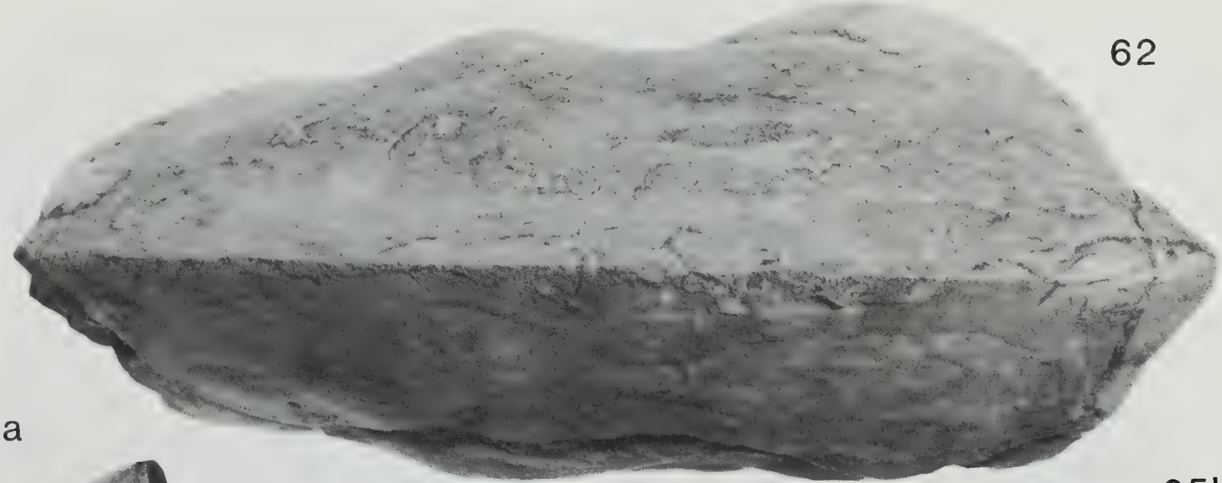
Material and occurrence. Twenty-nine specimens (C.83121–4, C.83486–8, UIN 427.1–21) from the Odukpani Formation (Lower Turonian), 34 km from Calabar.

Description. The shell attains a very large diameter, in excess of 500 mm. The umbilicus is tiny in the early stages but widens slightly later on. The whorl sides are convex, converging on the sharp venter. The umbilical shoulders are rounded and indistinct. The siphuncle is wide but constricted at the septal necks. The body chamber is about half a whorl in length.

In the early stages the whorl sides appear smooth, but since the material consists of weathered internal moulds it is unlikely that any fine ornament would be preserved. At a varying stage in ontogeny, but usually by a diameter of about 100 mm, definite ornamentation appears, consisting of broad bulge-like swellings on the flanks. These arise just outside the umbilical shoulder, reach their greatest height just dorsal of the mid-flank region and die out on the ventral part of the flank. There are six or seven bulges in each whorl. Some individuals show a weak ornament of elongate rib-like structures while others remain smooth at diameters in excess of 300 mm. Shell breadth also varies. Some specimens are compressed and tend to have a weak ornament; others rather inflated, in which it is generally more pronounced.

The sutures (Fig. 61) develop a highly sigmoidal pattern. They are variable in their details, sometimes being relatively simple, although the saddles may be elongated with constricted necks and globular endings.

Remarks. This material is similar to *Coilopoceras newelli* Benavides-Cáceres (1956: 473) from the Turonian of Peru, which also develops broad, elongate swellings at a varying stage in ontogeny. The Peruvian population also includes examples of inflated forms with a pronounced ornament (Benavides-Cáceres 1956: pl. 62, figs 5–7) along with weakly ornamented smooth variants (Benavides-Cáceres 1956: pl. 61, fig 5). The ornament in *C. newelli*, however, seems to be a little more rib-like and there appear to be slightly more of the bulges in each whorl.



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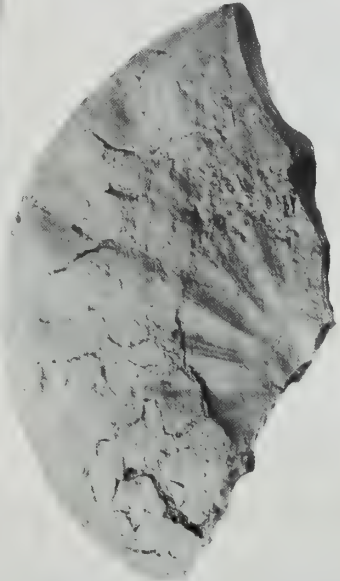
63a



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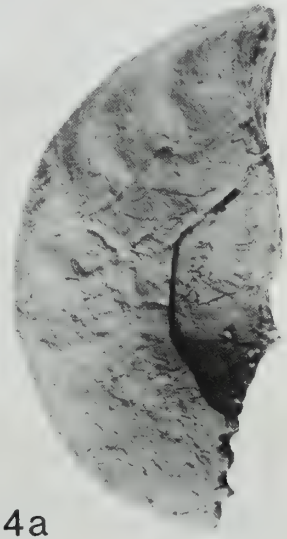

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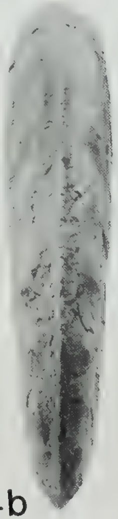

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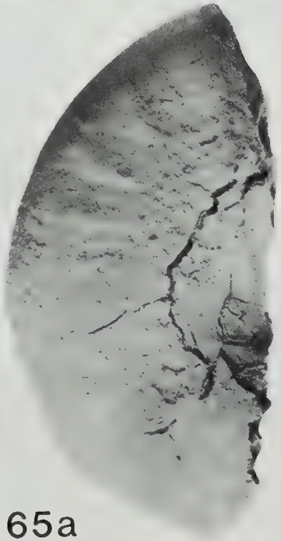
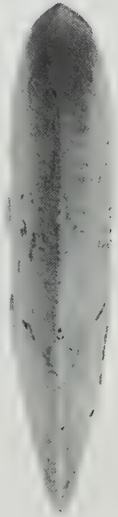


65a



65b

C. colleti Hyatt and *C. inflatum* Cobban & Hook from the middle part of the Turonian in the western interior of the U.S.A. (see Cobban & Hook 1980) are also similar to the present material. At large diameters *C. colleti* develops prominent lateral swellings (Cobban & Hook 1980: pl. 8; pl. 9; text-fig. 9) but these extend further ventrally than in the Nigerian material and this species also shows ventrolateral tubercles and ribbing in the early stages. *C. inflatum* develops an even more inflated adult shell (Cobban & Hook 1980: pl. 13) and its bulge-like ornament envelops more or less the whole of the whorl sides. *C. inflatum* also includes inflated, grossly ornamented variants and compressed smooth forms. Cobban & Hook (1980) interpreted the two varieties as dimorphs, the stouter forms sometimes dominating the population while at other localities there occur more even mixtures of the two types. This type of variable population structure thus seems to be common in *Coilopoceras*, but there seems to be no clear distinction between the two groups in the Nigerian material; rather they intergrade into one another.

Another highly inflated species is *C. discoideum* Barber (1957: 55; pl. 2, fig. 1; pl. 3, figs 1, 2; pl. 25, figs 1–4) but its ornament is stronger in the early whorls, the ribs broadening and disappearing in the adult stages.

Closely similar to the stout, grossly ornamented variants in *Coilopoceras* is the genus *Glebosoceras* Reyment (type species *Glebosoceras glebosum* Reyment 1954: 161; pl. 2, fig. 3; pl. 4, fig. 1). *Glebosoceras* also shows an ornament of broad bulge-like ribs and there seems to be little justification in separating it from *Coilopoceras*.

Fayose (1977: 235, fig. 5) described specimens from the Odukpani Formation as *Hoplitoides ingens* (von Koenen). These also show the bulbous ornament characterizing the present material and may be conspecific.

Family **SPHENODISCIDAE** Hyatt, 1900

Genus ***SPHENODISCUS*** Meek, 1871

Type species. *Ammonites lobata* Tuomey, 1856 (= *A. lenticularis* Owen, 1852 *non* Young & Bird, 1828); by the original designation of Meek, 1871.

Sphenodiscus lobatus (Tuomey) ***costatus*** Zaborski, 1982

Figs 63–65

1982 *Sphenodiscus lobatus costatus* Zaborski: 320, figs 22, 23, 26–35.

Material and occurrence. A total of 262 specimens from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. In addition to the material listed by Zaborski (1982: 320) these include UIN 424.156–201 and C.85270–5.

Remarks. This subspecies was described by Zaborski (1982: 320). The material considered included a number of small individuals showing variation in venter shape and ornamentation. These differences were thought to represent individual variation but further collections suggest the existence of dimorphism in this form.

The majority of the specimens from the locality reach a large diameter, in excess of 200 mm. A number were figured by Zaborski (1982: figs 23, 26–34). Others, preserved at a smaller diameter, represent the inner whorls of such large specimens (see Zaborski 1982: fig. 35). A few individuals seem to represent a second group, but only six (C.83185, C.83188,

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Fig. 62 *Coilopoceras* aff. *newelli* Benavides-Cáceres. Odukpani Formation (Lower Turonian), 34 km from Calabar. C.83520, ×0·75, ventral view of a fairly broad, grossly ornamented variant. See also Figs 60, 61.

Figs 63–65 *Sphenodiscus lobatus costatus* Zaborski. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. Fig. 63a, b, C.85273, ×1. Fig. 64a, b. C.85271, ×1. Both are microconchs(?) showing early broadening of the venter and development of ornament on the whorl sides. Fig. 65a, b, C.85275, a possible microconch(?), ×1.

C.83190, C.85271, C.85273–4) can be placed in it with confidence. They reach a maximum diameter of 75–80 mm but, since they consist exclusively of internal moulds of the body chamber alone, adulthood cannot be demonstrated on the basis of sutural simplification or approximation. At diameters in excess of 40–50 mm the initially sharp venter broadens and becomes fastigiate with a definite keel evident, or becomes broadly rounded. Broad, bullate rib-like structures develop; they are most pronounced ventrally and usually expanded into prominent ventrolateral tubercles. Although adulthood cannot be proved, it is possible that these specimens represent the microconch of this subspecies. The macroconch(?) retains a sharp venter and smooth flanks to a late stage in ontogeny (Zaborski 1982: 322).

Some problematical specimens show intermediate characters (see Zaborski 1982: fig. 22; Fig. 65a, b). They may represent microconchs(?) with a relatively narrow venter or alternatively some of the macroconchs(?) may show a subdued ornament in their early growth stages.

Dimorphism has previously been unknown in *Sphenodiscus*. *S. pleurisepta* (Conrad) develops pronounced ornamentation (Hyatt 1903: pl. 3, figs 7–15; pl. 4, figs 1, 2; pl. 5, figs 1–3; pl. 6, fig. 6), as does the related genus *Coahuilites* Böse (1927: 279), which shows a broad venter in its later growth stages. Both, however, reach a considerably larger size than the microconchs(?) described here.

Correlation and palaeogeography

Until the creation of the roadside cuttings described here, knowledge of the Cenomanian in southern Nigeria had been rudimentary. Reyment (1956, 1965), however, attempted a broad biostratigraphic subdivision of the Nigerian Cenomanian based upon ammonites. He proposed two zones: a lower 'Zone of *Euhystrichoceras occidentale* Reyment' containing, in addition to the nominal species, *Desmoceras* (*Pseudouhligella*) *calabarense* Reyment, *D.* (*D.*) *latidorsatum* (Michelin) and *Phylloceras* cf. *velledae* (Michelin); and an upper 'Zone of *Turrilites scheuchzerianus*' also containing *T. costatus*, *Forbesiceras sculptum* Crick, *F.* aff. *conlini* Stephenson, *Acompsoceras subwaterloti* Venzo, *Acanthoceras quadratum nigeriense* Reyment, *Calycoceras*, *Metoicoceras* and *Sharpeiceras*. The presence of *Euhystrichoceras* suggests a Lower Cenomanian age for his lower zone (see review of this genus in Kennedy & Wright 1981), but the upper zone contains forms characteristic of each Cenomanian substage. The existence of the Lower Cenomanian was confirmed by Förster (1978) and Förster & Scholz (1979), who reported basal Cenomanian ammonites in the Mfamosing Quarry just to the east of the present road section (see Fig. 2, p. 5). This quarry works a limestone (= 'Lower Limestone' of Murat (1972: 256); Mfamosing Limestone Formation of Petters (1982)) in the basal part of the Odukpani Formation which locally reaches a thickness of some 100 m. At Mfamosing the limestone is largely without ammonites, but towards the top it yields *Mortoniceras*. The upper surface of the limestone is an eroded hardground with a condensed horizon above containing a mixture of uppermost Albian and Lower Cenomanian ammonites (Förster & Scholz 1979: 111). The upper surface of this limestone can therefore be taken as locally representing the Albian–Cenomanian boundary. Large blocks, the remnants after dissolution of an algal biosparite similar to parts of the Mfamosing limestone, occur in the present road section immediately below the shales yielding fauna 1 described here. These shales can be assigned a definite Lower Cenomanian age on the basis of *Sharpeiceras laticlavium nigeriense*. Correlation with the *Hypoturrilites carcitanensis* or *Mantelliceras saxbii* Zone in southern England is most probable since both contain *S. laticlavium*. Faunas 2 and 3 described here may also be of Lower Cenomanian age. Fauna 2 contains *Puzosia* sp., *Acompsoceras* aff. *renevieri* and another *Acompsoceras* (C.83497) which shows umbilical bullae and a weakly ornamented venter, being close to *A. essendiense* (Schlüter 1871: 3; pl. 1, figs 5–7). Both of these *Acompsoceras* occur in the Lower Cenomanian of southern England (Kennedy 1971, Kennedy & Hancock 1978), although they may range higher. The *Forbesiceras* in fauna 3 is specifically indeterminate and cannot be accurately dated. The full extent and faunal content of the Lower Cenomanian part of the

Odukpani Formation is, therefore, still to be determined and detailed correlation with other areas is not yet possible. Similarly the age of the clastics of the Awi Formation and, indeed, that of the earliest sediments in the Calabar region remains unresolved. There are, however, reports of possible pre-Albian marine sediments in the shallow subsurface close to the Mfamosing Quarry (Ramanathan & Kumaran 1981).

A large part of the present material comes from the Middle Cenomanian portion of the Odukpani Formation and considerably enlarges our knowledge of it. In southern England and northern France the Middle Cenomanian (Zone of *Acanthoceras rhotomagense*) can be divided into three assemblage zones (see Kennedy 1971, Kennedy & Hancock 1977, 1978, Juignet & Kennedy 1976): a lower Zone of *Turrilites costatus*, a middle Zone of *T. acutus* and an upper Zone of *Acanthoceras jukesbrownei*. These horizons have sufficient faunal similarity to the Calabar region to allow detailed correlation. Those parts of the Odukpani Formation containing faunas 4, 5, 8 and 9, described here, correlate with the *costatus* and *acutus* Zones as they have the following species in common: *Turrilites costatus, T. acutus, T. scheuchzerianus, Anagaudryceras involvulum, Euomphaloceras inerme, E. cunningtoni* and *Forbesiceras obtectum*. The lower beds (with faunas 4 and 5) equate with the *costatus* Zone; the nominal species, *E. inerme* and early members of the *E. cunningtoni* group indicate this zone, probably the top part of it (see Kennedy 1971: 94, 96; Kennedy & Hancock 1977: 135). The Nigerian *E. inerme* often resembles *Acanthoceras rhotomagense* var. *sussexiense*, typical of the *costatus* Zone in north-west France (Kennedy & Hancock 1970). The *T. costatus* in fauna 5 are transitional to *T. acutus*, suggesting a position close to the boundary of the *costatus* and *acutus* Zones. The upper beds (with faunas 8 and 9) seem to equate with the *acutus* Zone. Fauna 8 includes the nominal species and *Forbesiceras obtectum* which occurs in this zone. The material referred here to *Calycoceras annulatum* seems to be most closely related to *Calycoceras* of the *newboldi* group, characteristic of the *acutus* Zone and younger strata in western Europe. In Normandy *Anagaudryceras involvulum* is known only from the *costatus* Zone (Juignet & Kennedy 1976), but its presence in younger strata in the Odukpani Formation is of little consequence, as it appears to have a long range: it has been described from the Turonian of Angola (Howarth 1966). Fauna 9 contains two specimens (C.85247, UIN 486.1) transitional between *Euomphaloceras cunningtoni cunningtoni* and *E. cunningtoni alatum*, but closer to the latter. Their associated *Acanthoceras robustum* suggests correlation with the *acutus* Zone (see p. 35). This fauna is, in fact, very close in age to, though probably slightly older than, fauna 8 of which *E. cunningtoni alatum* is a major element. Its westerly position in the road section is because folding has repeated the strata.

None of the diagnostic species of the European *jukesbrownei* Zone occurs in the Nigerian collection. Instead, the succeeding beds (with fauna 7) in the Calabar section (occurring east of those with fauna 8 as a result of folding) contain *Acanthoceras amphibolum*. This species provides an important point of reference with North American faunas. In the western interior of the U.S.A., *A. amphibolum* is the index for a zone in the upper part of the Middle Cenomanian (Cobban & Scott 1972: table 4; Kauffman *et al.* 1978). It also occurs at one level in the Japanese Middle Cenomanian (Matsumoto, Okada, Hirano & Tanabe 1978: 4); Kennedy & Hancock (1977: 135) tentatively correlated this horizon with the *jukesbrownei* Zone in Europe. The Nigerian sequence suggests that this is indeed correct, the *A. amphibolum* beds here appearing to correlate with the basal part of the *jukesbrownei* Zone. Middle Cenomanian faunas from the western interior have little else in common with Nigeria, only members of the *E. cunningtoni* group inviting immediate comparison. Forms similar to *E. cunningtoni cunningtoni* occur in the oldest undoubted Cenomanian in the western interior, the Thatcher Limestone Member of the Graneros Shale in south-eastern Colorado (Cobban & Scott 1972: 70; pl. 40; Kauffman *et al.* 1978: 11), belonging in the Zone of *Calycoceras* (*Conlinoceras*) *tarrantense* (Adkins). *Turrilites acutus* is also present here. This zone seems to correspond with the upper part of the *costatus* Zone or, more probably, the lower part of the *acutus* Zone in western Europe. The most nearly contemporaneous part of the Odukpani Formation is that yielding fauna 5. Overlying the Zone of *C. tarrantense* in the western interior there is a zone characterized by *Acanthoceras granerosense* below and *A.*

muldoonense above. In Colorado, forms close to *Euomphaloceras cunningtoni lonsdalei* are associated with *A. muldoonense* (Cobban & Scott 1972: pl. 42; Kauffman *et al.* 1978: 11), which seems to be contemporaneous with *E. cunningtoni alatum* in Nigeria. These two forms, both characterized by a reduction in the ventral ribbing and tuberculation, occur only a few metres below horizons with *Acanthoceras amphibolum.* Members of the *E. cunningtoni* group appear, therefore, to have some potential as stratigraphical indicators. In Japan and Texas, however, contradictory successions are reported. In Texas Young & Powell (1978: fig. 5) indicate *E. cunningtoni lonsdalei* appearing before *E. cunningtoni cunningtoni* and both as being at least partly contemporaneous with *A. amphibolum.* In Japan Matsumoto, Okada, Hirano & Tanabe (1978: 4) report *E. cunningtoni meridionale* in association with *A. amphibolum*, although in the Odukpani Formation it occurs considerably below the latter species.

Although faunal confirmation is lacking, structural evidence suggests that the highest Middle Cenomanian in the present section is that containing fauna 6 which occurs close to a synclinal axis. The only stratigraphically useful ammonite found here is *Forbesiceras obtectum*, which ranges through most of the Middle Cenomanian in north-west Europe (Kennedy & Hancock 1977: fig. 3).

Middle Cenomanian faunas from the Cuanza Basin in Angola have much in common with those of the Odukpani Formation. Near Novo Redondo, strata of *costatus* and *acutus* Zone age yield *Turrilites costatus, T. acutus*, large *Forbesiceras obtectum, Euomphaloceras* of the *cunningtoni* group and *Calycoceras annulatum* (Cooper 1973, 1978*a*). The Nigerian Middle Cenomanian, however, extends both higher and lower than the Novo Redondo beds. Thus *Euomphaloceras inerme* is unknown in the latter and the Angolan *E. cunningtoni* appears to be closer to the Nigerian *E. cunningtoni cunningtoni* than to the earlier *E. cunningtoni meridionale. Acanthoceras* cf. *granerosense* occurs at Novo Redondo (Cooper 1978*a*: 6), indicating beds older than the horizon with *A. amphibolum* in Nigeria. Lower Cenomanian occurs in the Novo Redondo area but, as in Nigeria, it is not sufficiently understood for detailed comparison. *Sharpeiceras laticlavium* (= *S. goliath* Haas) occurs east of Luanda (Haas 1942, Cooper 1978*a*: 6).

The Nigerian Cenomanian ammonites act as a palaeobiogeographical link between west European and Angolan faunas. According to Reyment & Tait (1972), the final opening of the South Atlantic Ocean, allowing free north–south faunal migration, took place as late as the end of the Lower Turonian. Kennedy & Cooper (1975), Kennedy & Cobban (1977: 76–80), Cooper (1978: 144–145), Förster (1978) and Förster & Scholz (1979) all presented evidence, based on ammonite distributions, to show that continuous migration was possible from late Albian times onwards. The present material strongly suggests that such migration took place during the Cenomanian. Particular mention may be made of *Acanthoceras amphibolum* and *Puzosia* (*Anapuzosia*) *dibleyi. A. amphibolum* is most typical of Texas and the western interior of the United States, otherwise occurring only in Japan and perhaps southern England. Its presence in southern Nigeria is difficult to explain unless migration from the North Atlantic was possible. *P.* (*A.*) *dibleyi* is known only from Angola and southern England. The presence of a very similar form in Nigeria, albeit in earlier strata, also suggests linkage.

Structural and faunal evidence suggests that an unconformity separates Middle Cenomanian from younger strata in the Odukpani Formation. Beds above this unconformity seem to dip uniformly to the south-west, those below are broadly folded. The youngest parts of the Middle Cenomanian and much of the Upper Cenomanian appear to be missing. The only Upper Cenomanian ammonite in the present collection is *Pseudocalycoceras* cf. *haughi*, but unfortunately the exact position of this specimen in the road section is uncertain. Reyment (1955: 47) described *Metoicoceras* aff. *ornatum* Moreman (= *M. geslinianum* (d'Orbigny): see review of this species in Kennedy *et al.* 1981: 60–76) from the Odukpani Formation, indicating the presence of terminal Cenomanian. This species is an important element of the *Sciponoceras gracile* faunal assemblage, which is recognizable almost world-wide (see Cooper 1978: 142–144). It would indeed be surprising if this assemblage were absent altogether, since one of its members, *Euomphaloceras septemseriatum*, occurs in the middle Benue Valley of central Nigeria (Offodile 1976, Offodile & Reyment 1976). But whether the *Pseudocalycoceras* from the Odukpani Formation is also of *S. gracile* Zone age is unproved; the sediments directly above the unconformity are not younger than this, which was a time of eustatic sea level rise and so a plausible date for the re-commencement of sedimentation. Nwachukwu (1972) and Olade (1975) also presented evidence for an intra-Cenomanian folding phase in southern Nigeria. Low dips occur in the Calabar region, but the Albian sediments outcropping in central south-eastern Nigeria are more strongly deformed, dips approaching the vertical being common. Although the intensity of the deformation is partly due to a later Santonian–Campanian tectonic episode, the possibility remains that marine Lower and Middle Cenomanian was removed from parts of southern Nigeria during the late Cenomanian folding.

The limestones in the uppermost part of the Odukpani Formation with *Kamerunoceras tinrhertense* and *Coilopoceras* aff. *newelli* are probably Lower Turonian. In Algeria *K. tinrhertense* is well dated as Lower Turonian (Collignon 1965: 198–199). Although *C. newelli* occurs in the upper part of the Turonian in Peru (Benavides-Cáceres 1956) and the related species *C. colleti* and *C. inflatum* are of mid and early late-Turonian age respectively in the United States (Cobban & Hook 1980), evidence from northern Nigeria (Barber 1957: 59, 61) indicates that *Coilopoceras* begins its range low in the Turonian and possibly even in the high Cenomanian. The Lower Turonian part of the Odukpani Formation is sometimes (see, for example, Petters 1980, 1982) referred to the Eze-Aku Formation. There is no real lithostratigraphic justification for this, however, and Reyment's (1955) original practice of including these strata in the Odukpani Formation is followed here.

Reyment (1956, 1965) divided the Nigerian Maastrichtian into three zones, from bottom to top: the Zone of *Libycoceras afikpoense* Reyment; the Zone of *Sphenodiscus studeri* Reyment; and the Zone of *Cordiceramus coxi* (Reyment). The Zone of *L. afikpoense* is, in fact, of Upper Campanian age but this species is an excellent indicator of the earliest marine Campanian in Nigeria. Reyment's upper two zones are unsatisfactory and, although said to be of Upper Maastrichtian age, they are not accurately dated and are almost certainly older.

The basal Nkporo Shale in the Calabar region falls into the Zone of *L. afikpoense*. The closest relative of this species, *L. ismaelis* (Zittel), begins its range in the lower part of the Zone of *Bostrychoceras polyplocum* in the Middle East (Reiss 1962). Like *L. afikpoense, L. ismaelis* occurs in association with *Sphenodiscus lobatus* (Picard 1929, Lewy 1977, Zaborski 1982) and a similar Upper Campanian age is most likely for the Nigerian species. None of the associated ammonites in the basal Nkporo Shale rules out an Upper Campanian age. *Pachydiscus egertoni* is said to be confined to the Campanian part of the Ariyalur Group in India (Sastry *et al.* 1968). The closely similar *P. neubergicus*, often considered to be a synonym of *P. egertoni* (see Matsumoto 1959: 43–44), is, however, an index for the Lower Maastrichtian in western Europe (Jeletzky 1951), although it may range both higher and lower (see Hancock & Kennedy 1981: 544). *Didymoceras cheyennense* (and indeed all the large *Didymoceras* of the western interior of the U.S.A.) occurs in the high Campanian (Gill & Cobban 1973: table 1; text-fig. 12). Along the Pacific coast of North America *D. hornbyense* and its allies are either of late Campanian or early Maastrichtian age (Usher 1952, Anderson 1958, Jones 1963). *Pseudoxybeloceras* (*Parasolenoceras*) occurs at various levels in the Campanian, typically being older than Upper Campanian (Matsumoto 1959: 164; Collignon 1969: 44, 47; Ward & Mallory 1977). *Gaudryceras varicostatum* ranges in age from Coniacian to Campanian (Kennedy & Klinger 1979: 138). Finally, Reyment (1955: 15) reported '*Bostrychoceras*' in the *Libycoceras afikpoense* Zone in south-east Nigeria. Thus the weight of evidence points to an Upper Campanian (*polyplocum* Zone) age for this horizon.

The overlying beds of the Nkporo Shale with *Libycoceras crossense* are probably equivalent to the upper part of the *polyplocum* Zone. *L. crossense* occurs below a horizon elsewhere in southern Nigeria (see Zaborski 1982) containing *L. dandense* (Howarth), of latest Campanian to earliest Maastrichtian age (Howarth 1965: 402–405).

The topmost part of the Nkporo Shale exposed in the Calabar section is probably Lower

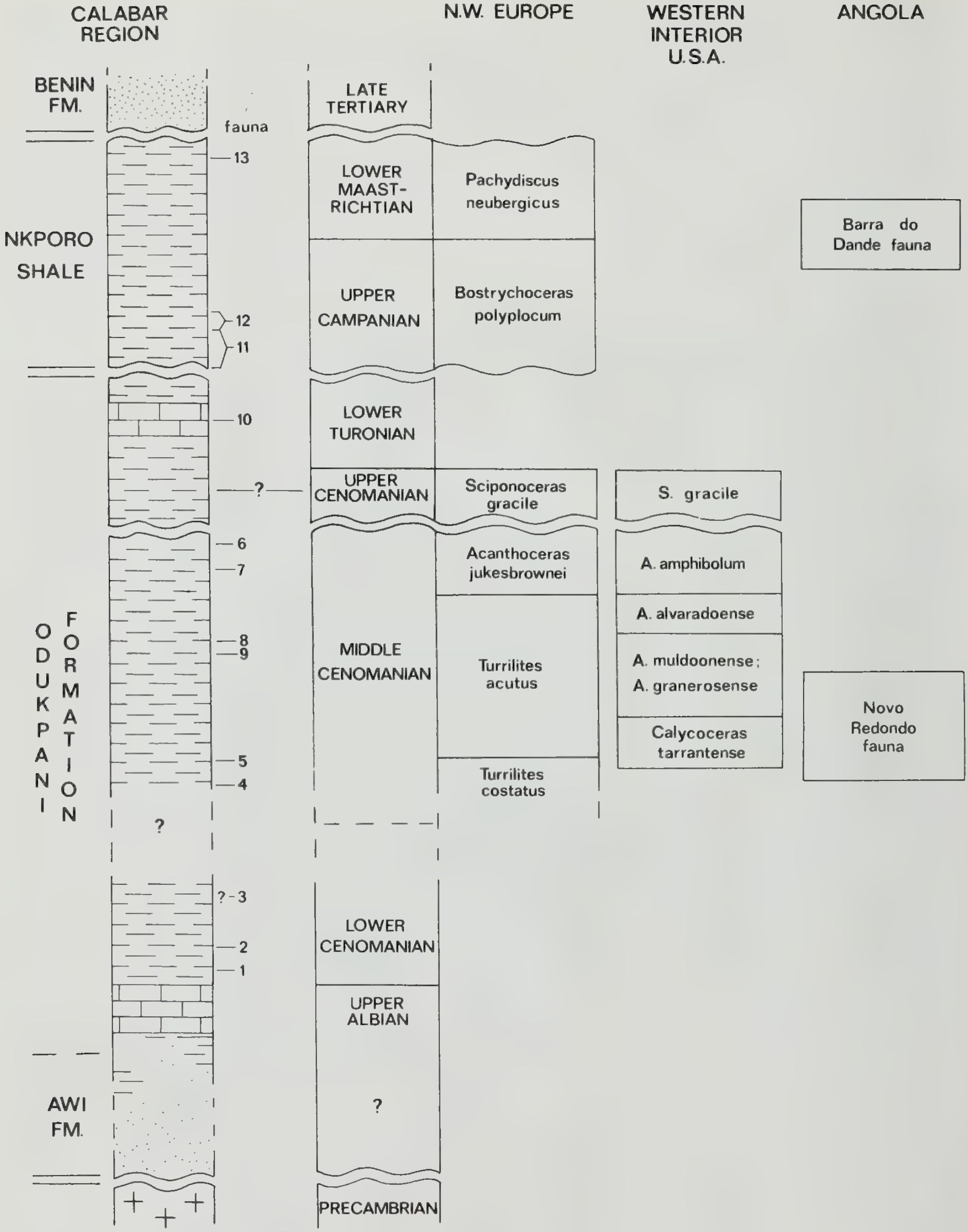
CALABAR REGION
N.W. EUROPE
WESTERN INTERIOR U.S.A.
ANGOLA
BENIN FM.
fauna
13
NKPORO SHALE
12
11
10
?
6
7
8
9
5
4
?
?-3
2
1
ODUKPANI FORMATION
AWI FM.
LATE TERTIARY
LOWER MAAST-RICHTIAN
Pachydiscus neubergicus
UPPER CAMPANIAN
Bostrychoceras polyplocum
LOWER TURONIAN
UPPER CENOMANIAN
Sciponoceras gracile
S. gracile
MIDDLE CENOMANIAN
Acanthoceras jukesbrownei
A. amphibolum
A. alvaradoense
Turrilites acutus
A. muldoonense; A. granerosense
Calycoceras tarrantense
Turrilites costatus
LOWER CENOMANIAN
UPPER ALBIAN
?
PRECAMBRIAN
Barra do Dande fauna
Novo Redondo fauna

Fig. 66 Generalized sedimentary sequence (not to scale) exposed in the road section north of Calabar and its correlation with north-west Europe, the western interior of the United States and Angola. Zonation in north-west Europe follows Kennedy (1971), Kennedy & Hancock (1978) and Juignet & Kennedy (1976). That for the western interior of the U.S.A. follows Kauffman *et al.* (1978). For Angola, the Barra do Dande fauna is that described by Howarth (1965); the Novo Redondo fauna is that described by Cooper (1973, 1978*a*).

Maastrichtian. *Sphenodiscus*, a dominantly Maastrichtian genus, is abundant here while *Pachydiscus dossantosi* has its closest affinities with European Lower Maastrichtian pachydiscids, particularly *P. gollevillensis*. This age is in accordance with the evidence provided by the associated inoceramid bivalves *Cordiceramus coxi* (Reyment), *Trochoceramus radiosus* (Quaas) and *Endocostea pteroides* (Giers) which range from Upper Campanian to Lower Maastrichtian (A. Dhondt and N. J. Morris, personal communication).

Species of *Libycoceras* provide the most promising basis for correlation in the Nigerian late Campanian and early Maastrichtian. Three zones can be recognized based on the ranges of the successive species *L. afikpoense*, *L. crossense* and *L. dandense* (see Zaborski 1983). These species span the *polyplocum* Zone, with *L. dandense* probably extending into the basal part of the *Pachydiscus neubergicus* Zone. The Zone of *L. afikpoense* is present in the Gombe region of north-east Nigeria, from where Reyment (1955: 90; pl. 19, fig. 3; pl. 20, fig. 4) described juvenile specimens which probably belong to this species. The Zone of *L. crossense* is represented in the Dukamaje Formation of north-west Nigeria which contains forms which are almost certainly conspecific (Zaborski 1982: 312). These occurrences add weight to arguments in favour of a late Campanian marine link between the Gulf of Guinea and the Tethys (see review of this subject in Reyment, 1980), the faunal evidence for which has been weak hitherto.

'Sphenodiscus' studeri Reyment (1957) may well be closely related to *Libycoceras dandense* (see Zaborski 1982: 325) and a basal Maastrichtian age seems most probable for this species. Reyment's youngest Maastrichtian index species, *Cordiceramus coxi*, occurs in the topmost marine band of the Nkporo Shale in the Calabar section, for which a Lower Maastrichtian age has been suggested above. Neither of Reyment's upper two zones, therefore, seems to be Upper Maastrichtian. The outcropping parts of this substage are dominantly regressive in Nigeria.

Figure 66 shows the generalized sedimentary sequence in the Calabar region and its correlation with north-west Europe, the western interior of the United States and Angola.

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References

Adeleye, D. R. & Fayose, E. A. 1978. Stratigraphy of the type section of Awi Formation, Odukpani area, southeastern Nigeria. *J. Min. Geol.*, Ibadan, **15:** 33–37.

Adkins, W. S. 1928. Handbook of Texas Cretaceous fossils. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **2838:** 1–303, pls 1–37.

—— 1929. Some Upper Cretaceous Taylor ammonites from Texas. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **2901:** 203–211, pls 5, 6.

Anderson, F. M. 1902. Cretaceous deposits of the Pacific Coast. *Proc. Calif. Acad. Sci.*, San Francisco, (3) **2:** 1–154, pls 1–12.

—— 1938. Lower Cretaceous deposits in California and Oregon. *Spec. Pap. geol. Soc. Am.*, New York, **16:** 1–339, pls 1–84.

—— 1958. Upper Cretaceous of the Pacific Coast. *Mem. geol. Soc. Am.*, New York, **71:** 1–378, pls 1–75.

Arkell, W. J. *et al.* 1957. Mollusca 4. Cephalopoda, Ammonoidea. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **L.** 490 pp., text-figs. Lawrence, Kansas.

Barber, W. 1957. Lower Turonian ammonites from north-eastern Nigeria. *Bull. geol. Surv. Nigeria*, Kaduna, **26:** 1–86, pls 1–35.

Basse, E. 1940. Les céphalopodes crétacés des massifs côtiers syriens. Pt. 1. *Notes Mém. Ht.-Comm. Syrie Liban,* Paris, **3:** 412–490, pls 1–9.

Bayle, E. 1878. Fossiles principaux des Terrains. *Explication Carte géol. Fr.,* Paris, **4** (1): atlas of 158 pls.

Benavides-Cáceres, V. E. 1956. Cretaceous system in northern Peru. *Bull. Am. Mus. nat. Hist.,* New York, **108:** 353–494, pls 31–66.

Bosc, L. A. G. 1802. Historie naturelle des coquilles. *In* Buffon, G. L. L. de, *Historie naturelle de Buffon,* **5:** 1–255, pls 35–44. Paris.

Böse, E. 1927. Cretaceous ammonites from Texas and northern Mexico. *Bull. Univ. Tex. Bur. econ. Geol. Technol.,* Austin, **2748:** 143–312, pls 1–18.

Boule, M., Lemoine, P. & Thévenin, A. 1906–07. Paléontologie de Madagascar. III – Céphalopodes crétacés des environs de Diègo-Suarez. *Annls Paléont.,* Paris, **1:** 173–192, pls 14–20 (1906); **2:** 1–56, pls 1–8 (1907).

Brongniart, A. 1822. Sur quelques terrains de Craie hors du bassin de Paris. *In* Cuvier, G. & Brongniart, A., *Description géologique des environs de Paris* (nouv. éd.): 80–106. Paris.

Clark, D. L. 1965. Heteromorph ammonites from the Albian and Cenomanian of Texas and adjacent areas. *Mem. geol. Soc. Am.,* New York, **95:** 1–99, pls 1–24.

Cobban, W. A. 1977. Characteristic marine molluscan fossils from the Dakota Sandstone and intertongued Mancos Shale, west central New Mexico. *Prof. Pap. U.S. geol. Surv.,* Washington, **1009:** 1–30, pls 1–21.

—— **& Hook, S. C.** 1980. The Upper Cretaceous ammonite family Coilopoceratidae Hyatt in the Western Interior of the United States. *Prof. Pap. U.S. geol. Surv.,* Washington, **1192:** 1–28, pls 1–21.

—— **& Scott, G. R.** 1972. Stratigraphy and ammonite fauna of the Graneros Shale and Greenhorn Limestone near Pueblo, Colorado. *Prof. Pap. U.S. geol. Surv.,* Washington, **645:** 1–108, pls 1–41.

Collignon, M. 1928–29. Les céphalopodes du Cénomanien pyriteaux de Diègo-Suarez, Paléontologie de Madagascar. *Annls Paléont.,* Paris, **17:** 139–160, pls 15–19 (1928); **18:** 1–56, pls 1, 2 (1929).

—— 1931. La faune du Cénomanien à fossiles pyriteaux du nord de Madagascar. *Annls Paléont.,* Paris, **20:** 43–104, pls 5–9.

—— 1933. Fossiles Cénomaniens d'Antsatramahavelona (Province d'Analalava, Madagascar). *Annls géol. Serv. Mines Madagascar,* Tananarive, **3:** 53–79, 6 figs, pls V–VI.

—— 1956. Ammonites néocrétacées du Menabe (Madagascar). IV. Les Phylloceratidae; V. Les Gaudryceratidae; VI. Les Tetragonitidae. *Annls géol. Serv. Mines Madagascar,* Tananarive, **23:** 1–106, pls 1–11.

—— 1963. *Atlas des fossiles caracteristiques de Madagascar (Ammonites).* **X** (Albien). xv+184 pp., pls 241–317. Service géologique, Tananarive.

—— 1964. *Atlas des fossiles caracteristiques de Madagascar (Ammonites).* **XI** (Cénomanien). xi+152 pp., pls 318–375. Service géologique, Tananarive.

—— 1965. Nouvelles ammonites néocrétacées sahariennes. *Annls Paléont.,* Paris, **51:** 162–202, 8 pls.

—— 1965*a. Atlas des fossiles caracteristiques de Madagascar (Ammonites).* **XIII** (Coniacien). vii+88 pp., pls 414–454. Service géologique, Tananarive.

—— 1966. Les céphalopodes crétacés du bassin côtier de Tarfaya. *Notes Mém. Serv. géol. Maroc,* Rabat, **175** (2): 7–148, pls 1–35.

—— 1969. *Atlas des fossiles caracteristiques de Madagascar (Ammonites).* **XV** (Campanien Inférieur). xi+216 pp., pls 514–606. Service géologique, Tananarive.

Cooper, M. R. 1973. Cenomanian ammonites from Novo Redondo, Angola. *Ann. S. Afr. Mus.,* Cape Town, **62:** 41–67, figs 1–13.

—— 1978. Uppermost Cenomanian–basal Turonian ammonites from Salinas, Angola. *Ann. S. Afr. Mus.,* Cape Town, **75:** 51–152.

—— 1978*a*. The mid-Cretaceous (Albian–Turonian) biostratigraphy of Angola. *Annls Mus. Hist. nat. Nice* **4** (XVI): 1–22, pls 1–6.

Crick, G. C. 1907. The Cephalopoda from the deposit at the north end of False Bay, Zululand. *In* Anderson, W., *Third and final report of the Geological Survey of Natal and Zululand:* 163–234, pls 10–15. London.

Diener, G. 1925. Ammonoidea neocretacea. *Fossilium Cat.,* Berlin, (1: Animalia) **29.** 244 pp.

Douvillé, H. 1904. Paléontologie, mollusques fossiles. *In* Morgan, J. de, *Mission scientifique en Perse* **3** (4): 191–380, pls 25–50. Paris.

—— 1931. Contributions à la géologie de l'Angola. Les ammonites de Salinas. *Bolm Mus. Lab. miner. geol. Univ. Lisb.* **1:** 17–46, pls 1–4.

Erni, A. 1944. Ein Cenoman-ammonit *Cunningtoniceras höltkeri* nov. spec. aus Neuguinea, nebst Bemerkungen über einige andere Fossilien von dieser Insel. *Eclog. geol. Helv.*, Basel, **37:** 468–475.

Fabre, S. 1940. Le Crétacé supérieur de la Basse-Provence occidentale. 1. Cénomanien et Turonien. *Annls Fac. Sci. Marseille* (2) **14:** 1–355, pls 1–10.

Fayose, E. A. 1977. Turonian fauna from east of Odukpani, S.E. Nigeria. *Bull. Inst. fond. Afr. noire,* Dakar, (A) **39:** 231–240.

Forbes, E. 1846. Report on the Cretaceous fossil invertebrates from southern India, collected by Mr Kaye and Mr Cunliffe. *Trans. geol. Soc. Lond.* (2) **7:** 97–174, pls 7–19.

Förster, R. 1978. Evidence for an open seaway between southern and northern proto-Atlantic in Albian times. *Nature, Lond.*, **272:** 158–159.

—— **& Scholz, G.** 1979. *Salaziceras nigerianum* n. sp. from southeast Nigeria: faunal evidence for an open seaway between northern and southern Atlantic in late Albian times. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **2:** 109–119.

Gabb, W. M. 1864–69. *Geological survey of California. Palaeontology.* **1** (4): 57–217, pls 9–32 (1864). **2:** 1–299, pls 1–36 (1869). Philadelphia.

Gill, J. R. & Cobban, W. A. 1973. Stratigraphy and geologic history of the Montana Group and equivalent rocks, Montana, Wyoming and North and South Dakota. *Prof. Pap. U.S. geol. Surv.*, Washington, **776:** 1–37.

Gill, T. 1871. Arrangement of the families of mollusks. *Smithson. misc. Collns,* Washington, **227.** xvi+ 49 pp.

Grossouvre, A. de 1894. Recherches sur la Craie Supérieure. **2,** Paléontologie. Les ammonites de la Craie supérieure. 264 pp., atlas of 39 pls. *Mém. Serv. Carte dét. géol. Fr.*, Paris.

Guéranger, E. 1867. *Album paléontologique du département de la Sarthe.* 20 pp., 25 pls. Le Mans.

Haas, O. 1942. Some Upper Cretaceous ammonites from Angola. *Am. Mus. Novit.*, New York, **1182:** 1–24.

—— 1963. *Paracanthoceras wyomingense* (Reagan) from the Western Interior of the United States and from Alberta (Ammonoidea). *Am. Mus. Novit.*, New York, **2151:** 1–19.

—— 1964. *Plesiacanthoceras*, new name for *Paracanthoceras* Haas, 1963, *non* Furon, 1935. *J. Paleont.*, Tulsa, **38:** 610.

Hancock, J. M. & Kennedy, W. J. 1981. Upper Cretaceous ammonite stratigraphy: some current problems. *In* House, M. R. & Senior, J. R. (eds), *The Ammonoidea:* 531–553. London (Academic Press, for the Systematics Association).

Hattin, D. E. 1965. Stratigraphy of the Graneros Shale (Upper Cretaceous) in Central Kansas. *Bull. Kans. Univ. geol. Surv.*, Lawrence, **178:** 1–83, pls 1–5.

—— 1968. *Plesiacanthoceras wyomingense* (Reagan) from Graneros Shale and Greenhorn Limestone (Upper Cretaceous) of central Kansas. *J. Paleont.*, Tulsa, **42:** 1084–1090.

Hauer, F. von 1858. Über die Cephalopoden der Gosauschichten. *Beitr. Paläont. Oest.*, Vienna, **1:** 7–14, pls 1–3.

—— 1866. Neue Cephalopoden aus den Gosaugebilden der Alpen. *Sber. Akad. Wiss. Wien* (I) **53:** 300–308, pls 1, 2.

Henderson, R. A. 1970. Ammonoidea from the Mata Series (Santonian–Maastrichtian) of New Zealand. *Spec. Pap. Palaeont.*, London, **6:** 1–82, pls 1–15.

Hoepen, E. C. N. van 1921. Cretaceous Cephalopoda from Pondoland. *Ann. Transv. Mus.*, Pretoria, **8:** 1–48, pls 1–11.

Howarth, M. K. 1965. Cretaceous ammonites and nautiloids from Angola. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **10** (10): 335–412, pls 1–13.

—— 1966. A mid-Turonian ammonite fauna from the Moçâmedes Desert, Angola. *Garcia de Orta,* Lisbon, **14:** 217–228, pls 1–3.

Hyatt, A. 1894. Phylogeny of an acquired characteristic. *Proc. Am. phil. Soc.*, Philadelphia, **32:** 349–647, pls 1–14.

—— 1900. Cephalopoda. *In* von Zittel K. A. (transl. Eastman, C. R.), *Textbook of Palaeontology,* **1:** 502–604. London.

—— 1903. Pseudoceratites of the Cretaceous. *Monogr. U.S. geol. Surv.*, Washington, **44:** 1–351, pls 1–47.

Imkeller, H. 1901. Die Kreidebildungen und ihre Fauna am Stallauer Eck und Enzenauer Kopf bei Tölz. *Palaeontographica,* Stuttgart, **48:** 1–64, pls 1–3.

Jeletzky, J. A. 1951. Die Stratigraphie und Belemnitenfauna des Obercampen und Maastricht Westfalens, Nordwestdeutschlands und Dänemarks sowie einige allgemeine Gliederungs-Probleme der jüngeren borealen Oberkreide Eurasiens. *Beih. geol. Jb.*, Hannover, **1:** 1–142, pls 1–7.

Jimbo, K. 1894. Beiträge zur Kenntnis der Fauna der Kreideformation von Hokkaidō. *Paläont. Abh.*, Jena, **6** (3): 149–194, pls 1–9.

Jones, D. L. 1963. Upper Cretaceous (Campanian and Maestrichtian) ammonites from southern Alaska. *Prof. Pap. U.S. geol. Surv.*, Washington, **432:** 1–53, pls 1–41.

Juignet, P. & Kennedy, W. J. 1976. Faunes d'ammonites et biostratigraphie comparée du Cénomanien de nord-ouest de la France (Normandie) et du sud de l'Angleterre. *Bull. trimest. Soc. géol. Normandie Amis Mus. Havre* **63** (2): 1–193, pls 1–34.

Kauffman, E. G., Cobban, W. A. & Eicher, D. L. 1978. Albian through Lower Coniacian strata, biostratigraphy and principal events, Western Interior, United States. *Annls Mus. Hist. nat. Nice* **4** (XXIII): 1–52, pls 1–17.

Kellum, L. B. & Mintz, L. W. 1962. Cenomanian ammonites from the Sierra de Tlahualilo, Coahuila, Mexico. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **13:** 267–287, pls 1–8.

Kennedy, W. J. 1971. Cenomanian ammonites from southern England. *Spec. Pap. Palaeont.*, London, **8:** 1–133, pls 1–64.

—— 1978. The middle Cretaceous of Zululand and Natal, eastern South Africa. *Annls Mus. Hist. nat. Nice* **4** (XVIII): 1–29, pls 1–6.

—— **& Cobban, W. A.** 1977. Aspects of ammonite biology, biogeography and biostratigraphy. *Spec. Pap. Palaeont.*, London, **17:** 1–94, pls 1–11.

—— **& Cooper, M. R.** 1975. Cretaceous ammonite distribution and the opening of the South Atlantic. *J. geol. Soc. Lond.* **131:** 283–288.

—— **& Hancock, J. M.** 1970. Ammonites of the genus *Acanthoceras* from the Cenomanian of Rouen, France. *Palaeontology*, London, **13:** 462–490, pls 88–97.

—— —— 1977. Towards a correlation of the Cenomanian sequences of Japan with those of north-west Europe. *Spec. Pap. palaeont. Soc. Japan*, Tokyo, **21:** 127–141.

—— —— 1978. The mid-Cretaceous of the United Kingdom. *Annls Mus. Hist. nat. Nice* **4** (V): 1–72, pls 1–30.

—— **& Juignet, P.** 1975. Présence du genre *Anagaudryceras* (Ammonoidea) dans le Cénomanien de Haute-Normandie. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1975** (3): 77–79.

——, —— **& Hancock, J. M.** 1981. Upper Cenomanian ammonites from Anjou and the Vendée, western France. *Palaeontology*, London, **24:** 25–84, pls 3–17.

—— **& Klinger, H. C.** 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **25** (4): 265–315, 1 pl., 12 text-figs.

—— —— 1979. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **31** (2): 121–174, pls 1–14.

—— **& Wright, C. W.** 1979. On *Kamerunoceras* Reyment, 1954 (Cretaceous Ammonoidea). *J. Paleont.*, Tulsa, **53:** 1165–1178, 4 pls.

—— —— 1981. *Euhystrichoceras* and *Algericeras*, the last mortoniceratine ammonites. *Palaeontology*, London, **24:** 417–435, pls 59–61.

Klinger, H. C. 1976. Cretaceous heteromorph ammonites from Zululand. *Mem. geol. Surv. Un. S. Afr.*, Pretoria, **69.** ix+142 pp., 43 pls.

Kossmat, F. 1895–98. Untersuchungen über die Südindische Kreideformation. *Beitr. Paläont. Geol. Öst.-Ung.*, Vienna and Leipzig, **9:** 97–203, pls 15–25 (1895); **11:** 1–46, pls 1–8 (1897); **12:** 89–152, pls 14–19 (1898).

Lamarck, J. B. P. A. de M. de 1801. *Système des animaux sans vertèbres.* viii+432 pp. Paris.

Lewy, Z. 1969. Late Campanian heteromorph ammonites from southern Israel. *Israel J. Earth Sci.*, Jerusalem, **18:** 109–135, pls 1–4.

—— 1977. Late Campanian pseudoceratites from Israel and Jordan. *J. palaeont. Soc. India*, Lucknow, **20:** 244–250, 1 pl.

Mantell, G. A. 1822. *The fossils of the South Downs.* xvii+327 pp. 42 pls. London.

Matsumoto, T. 1954. Family Puzosiidae from Hokkaido and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **5:** 69–118, pls 9–32.

—— 1959. Upper Cretaceous ammonites from California. Part 2. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **Spec. vol. 1:** 1–172, pls 1–41.

—— 1967. Evolution of the Nostoceratidae (Cretaceous heteromorph ammonoids). *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **18:** 331–347, pls 18–19.

——, **Kawashita, Y., Fujishima, Y. & Miyauchi, T.** 1978. *Mammites* and allied ammonites from the Cretaceous of Hokkaido and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **24:** 1–24, pls 1–6.

——, **Muramoto, T. & Takahashi, T.** 1969. Selected acanthoceratids from Hokkaido. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **19:** 251–296, pls 25–38.

—— **& Obata, I.** 1966. An acanthoceratid ammonite from Sakhalin. *Bull. natn. Sci. Mus. Tokyo* **9:** 43–52, 4 pls.

——, **Okada, H., Hirano, B. & Tanabe, K.** 1978. Mid-Cretaceous zonation in Japan. *Annls Mus. Hist. nat. Nice* **4** (XXXIII): 1–23.

—— **& Saito, R.** 1954. A nearly smooth pachydiscid from Hokkaido, Japan. *Jap. J. Geol. Geogr.*, Tokyo, **24:** 87–92, pls 9–11.

——, —— **& Fukada, A.** 1957. Some acanthoceratids from Hokkaido. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **6:** 1–45, pls 1–18.

Maury, C. J. 1930. O Cretaceo da parahyba do norte. *Monografias Div. geol. miner. Bras.*, Rio de Janeiro, **8:** 1–305, pls 1–35.

Meek, F. B. 1871. Preliminary paleontological report, consisting of lists of fossils, with descriptions of some new types. *Rep. U.S. geol. geogr. Surv. Territ.*, Washington, **4** (= *Prelim. Rep. U.S. geol. Surv. Wyoming*): 287–318.

—— 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country. *Rep. U.S. geol. Surv. Territ.*, Washington, **9.** 629 pp., 45 pls.

—— **& Hayden, F. V.** 1856. Descriptions of new species of Gasteropoda and Cephalopoda from the Cretaceous formation of Nebraska Territory. *Proc. Acad. nat. Sci. Philad.* **8:** 70–72.

Moreman, W. L. 1942. Paleontology of the Eagle Ford Group of north and central Texas. *J. Paleont.*, Tulsa, **16:** 192–220, pls 31–34.

Morrow, A. L. 1935. Cephalopods from the Upper Cretaceous of Kansas. *J. Paleont.*, Menasha, **9:** 463–473, pls 49–53.

Murat, R. C. 1972. Stratigraphy and palaeogeography of the Cretaceous and Lower Tertiary in southern Nigeria. *In* Dessauvagie, T. F. J. & Whiteman, A. J. (eds), *African Geology:* 251–266. Ibadan.

Neumayr, M. 1875. Die Ammoniten der Kreide und die Systematik der Ammonitiden. *Z. dt. geol. Ges.*, Berlin, **27:** 854–892.

Nwachukwu, S. O. 1972. The tectonic evolution of the southern portion of the Benue Trough, Nigeria. *Geol. Mag.*, Cambridge, **109:** 411–419.

Offodile, M. E. 1976. The geology of the Middle Benue, Nigeria. *Spec. Vol. palaeont. Inst. Univ. Uppsala* **4:** 1–166, pls 1–20.

—— **& Reyment, R. A.** 1976. Stratigraphy of the Keana-Awe area of the Middle Benue region of Nigeria. *Bull. geol. Instn Univ. Uppsala* (n.s.) **7:** 37–66, figs 1–41.

Olade, M. A. 1975. Evolution of Nigeria's Benue Trough (aulacogen): a tectonic model. *Geol. Mag.*, Cambridge, **112:** 575–583.

Olsson, A. A. 1944. Contributions to the paleontology of northern Peru. The Cretaceous of the Paita region. *Bull. Amer. Paleont.*, Ithaca, **28:** 1–164, pls 1–17.

Orbigny, A. d' 1840–42. *Paléontologie français, Terrains crétacées.* **1,** *Céphalopodes:* 1–120 (1840), 121–430 (1841), 431–662 (1842), 148 pls. Paris.

Owen, D. D. 1852. Descriptions of some new and imperfectly known genera and species of organic remains, collected during the geological surveys of Wisconsin, Iowa and Minnesota. *In* Owen, D. D., *Report of a geological survey of Wisconsin, Iowa and Minnesota; and incidentally of a portion of Nebraska Territory:* 573–587. Philadelphia.

Passy, A. 1832. *Description géologique du département de la Seine-inférieure.* 371 pp., 20 pls. Rouen.

Pervinquière, L. 1907. *Carte géologique de la Tunisie. Études de paléontologie tunisienne,* **1.** *Céphalopodes des terrains secondaires.* 438 pp., 27 pls. Paris.

Petters, S.W. 1980. Biostratigraphy of Upper Cretaceous foraminifera of the Benue Trough, Nigeria. *J. foramin. Res.*, Washington, **10:** 191–204, 2 pls.

—— 1982. Central West African Cretaceous–Tertiary benthic foraminifera and stratigraphy. *Palaeontographica,* Stuttgart, (A) **179:** 1–104, pls 1–15.

Picard, L. 1929. On Upper Cretaceous (chiefly Maestrichtian) Ammonoidea from Palestine. *Ann. Mag. nat. Hist.*, London, (10) **3:** 433–456, pls 9, 10.

Pictet, F. J. 1863. Discussion sur les variations et les limites de quelques espèces d'ammonites des groupes de *A. rhotomagensis* et *mantelli.* Mélanges Paléontologiques. *Mém. Soc. Phys. Hist. nat. Genève* **17:** 22–58, pls 1–8.

Ramanathan, R. M. & Kumaran, K. P. N. 1981. Age and palaeoecology of M-1 well in Calabar Flank, south-eastern Nigeria. *J. Min. Geol.*, Ibadan, **18:** 163–171.

Reiss, Z. 1962. Stratigraphy of phosphate deposits in Israel. *Bull. geol. Surv. Israel,* Jerusalem, **34:** 1–23.

Renz, O. 1972. Die Gattungen *Puzosia* Bayle, *Bhimaites* Matsumoto und *Desmoceras* Zittel (Ammonoidea) im Oberen Albien Venezuelas. *Eclog. geol. Helv.*, Basel, **65:** 701–724, pls 1–10.

Reyment, R. A. 1954. New Turonian (Cretaceous) ammonite genera from Nigeria. *Colon. Geol. Miner. Resour.*, London, **4:** 149–164, pls 1–4.

—— 1954*a*. Some new Cretaceous ammonites from Nigeria. *Colon. Geol. Miner. Resour.*, London, **4:** 248–270, pls 1–5.

—— 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria,* Kaduna, **25:** 1–112, pls 1–24.

—— 1956. On the stratigraphy and palaeontology of the Cretaceous of Nigeria and the Cameroons, British West Africa. *Geol. För. Stockh. Förh.* **78:** 17–96.

—— 1957. Über einige wirbellose Fossilien aus Nigerien und Kamerun, Westafrika. *Palaeontographica,* Stuttgart, (A) **109:** 41–70, pls 7–11.

—— 1965. *Aspects of the geology of Nigeria.* 145 pp., 18 pls. Ibadan.

—— 1980. Biogeography of the Saharan Cretaceous and Paleocene epicontinental transgressions. *Cret. Res.*, London, **1:** 299–327.

—— **& Tait, E. A.** 1972. Biostratigraphical dating of the early history of the South Atlantic Ocean. *Phil. Trans. R. Soc.*, London, (B) **264:** 55–95, pls 3–5.

Sastry, M. V. A., Rao, B. R. J. & Mamgain, V. D. 1968. Biostratigraphic zonation of the Upper Cretaceous formation of Trichinopoly district, S. India. *Mem. geol. Soc. India,* Bangalore, **2:** 10–17.

Schlüter, C. 1871–76. Die Cephalopoden der oberen deutschen Kreide. *Palaeontographica,* Stuttgart, **21:** 1–24, pls 1–18 (1871); **21:** 25–120, pls 19–35 (1872); **24:** 121–264, pls 36–55 (1876).

Seunes, J. 1890. Contributions à l'étude des céphalopodes du Crétacé supérieure de la France. 1, Ammonites du calcaire à *Baculites* du Cotentin. *Mém. Soc. géol. Fr. Paléont.*, Paris, **1:** 1–7, pls 1, 2.

Sharpe, D. 1853–57. Description of the fossil remains of Mollusca found in the Chalk of England. **1,** Cephalopoda: 1–26, pls 1–10 (1853), 27–36, pls 11–16 (1855), 37–68, pls 17–21 (1857). *Palaeontogr. Soc. (Monogr.),* London.

Shimizu, S. 1934. Ammonites. *In* Shimizu, S. & Obata, T., *Cephalopoda. Iwanami's lecture series of geology and palaeontology.* 137 pp. Tokyo. [In Japanese].

—— 1935. The Upper Cretaceous cephalopods of Japan. Part 1. *J. Shanghai Sci. Inst.* (II) **2:** 159–226.

Solger, F. 1904. Die Fossilien der Mungokreide in Kamerun und ihre geologische Bedeutung, mit besonderer Berücksichtigung der Ammonitiden. *In* Esch, E., Solger, F., Oppenheim, M. & Jäkel, O., *Beiträge zur Geologie von Kamerun:* 83–242, pls 3–5. Stuttgart.

Sowerby, J. de C. 1823–46. *The mineral conchology of Great Britain* (cont.) **4** (*pars*)-**7,** pls 384–648. London.

Spath, L. F. 1922. On the Senonian ammonite fauna from Pondoland. *Trans. R. Soc. S. Afr.*, Cape Town, **10:** 113–147, pls 5–9.

—— 1923–43. A monograph of the Ammonoidea of the Gault. 787 pp., 72 pls. *Palaeontogr. Soc. (Monogr.),* London.

—— 1923*a*. Appendix II. On the Ammonite Horizons of the Gault and Contiguous Deposits. *Summ. Progr. geol. Surv. Lond.* **1922:** 139–149.

—— 1925. On Upper Albian Ammonoidea from Portuguese East Africa. With an appendix on Upper Cretaceous ammonites from Maputoland. *Ann. Transv. Mus.*, Pretoria, **11:** 179–200, pls 28–37.

—— 1926. On new ammonites from the English Chalk. *Geol. Mag.*, London, **63:** 77–83.

Stephenson, L. W. 1941. The larger invertebrate fossils of the Navarro Group of Texas. *Publs Bur. econ. Geol. Univ. Tex.*, Austin, **4101:** 1–641, pls 1–95.

—— 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. *Prof. Pap. U.S. geol. Surv.*, Washington, **242:** 1–226, pls 1–59.

—— 1955. Basal Eagle Ford fauna (Cenomanian) in Johnson and Tarrant Counties. *Prof. Pap. U.S. geol. Surv.*, Washington, **274–c:** 53–67, pls 4–7.

Stoliczka, F. 1863–66. The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. geol. Surv. India Palaeont. indica,* Calcutta, (3) **1:** 41–56, pls 26–31 (1863); **2–5:** 57–106, pls 32–54 (1864); **6–9:** 107–154, pls 55–80 (1865); **10–13:** 155–216, pls 81–94 (1866).

Thomel, G. 1969. Réflexions sur les genres *Eucalycoceras* et *Protacanthoceras* (Ammonoidea). *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **268:** 649–652.

—— 1972. Les Acanthoceratidae Cénomaniens des chaînes subalpines méridionales. *Mém. Soc. géol. Fr.*, Paris, (n.s.) **116:** 1–204, pls 1–85.

Tuomey, M. 1856. Description of some new fossils from the Cretaceous rocks of the southern states. *Proc. Acad. nat. Sci. Philad.* **7:** 162–172.

Usher, J. L. 1952. Ammonite fauna of the Upper Cretaceous of Vancouver Island, British Columbia. *Bull. geol. Surv. Can.*, Ottawa, **21:** 1–182, pls 1–30.

Venzo, S. 1936. Cefalopodi del Cretacea medio-superiore dello Zululand. *Palaeontogr. ital.*, Pisa, **36:** 59–133, pls 5–12.

Ward, P. D. & Mallory, V. S. 1977. Taxonomy and evolution of the lytoceratid genus *Pseudoxybeloceras* and relationship to the genus *Solenoceras*. *J. Paleont.*, Tulsa, **51:** 606–618, 3 pls.

Wedekind, R. 1916. Uber Lobus, Suturallobus und Inzision. *Centbl. Miner. Geol. Paläont.*, Stuttgart, **1916** (8): 185–195.

Whiteaves, J. F. 1895. Notes on some fossils from the Cretaceous rocks of British Columbia. *Can. Rec. Sci.*, Montreal, **6:** 313–318.

—— 1903. On some additional fossils from the Vancouver Cretaceous, with a revised list of species therefrom. *Mesozoic Fossils* **1** (5): 309–415, pls 40–51. Geological Survey of Canada, Ottawa.

Wiedmann, J. 1962. Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1, Phylloceratina, Lytoceratina. *Palaeontographica*, Stuttgart, (A) **118:** 119–237, pls 8–14.

—— **& Kauffman, E. G.** 1978. Mid-Cretaceous biostratigraphy of northern Spain. *Annls Mus. Hist. nat. Nice* **4** (III): 1–34, pls 1–12.

—— **& Kullman, J.** 1981. Ammonoid sutures in ontogeny and phylogeny. *In* House, M. R. & Senior, J. R. (eds), *The Ammonoidea:* 215–255. London (Academic Press, for the Systematics Association).

Wright, C. W. 1952. A classification of the Cretaceous ammonites. *J. Paleont.*, Tulsa, **26:** 213–222.

—— 1963. Cretaceous ammonites from Bathurst Island, Northern Australia. *Palaeontology*, London, **6:** 597–614, pls 81–89.

—— **& Kennedy, W. J.** 1981. The Ammonoidea of the Plenus Marls and the Middle Chalk. 148 pp., 32 pls. *Palaeontogr. Soc. (Monogr.)*, London.

—— **& Matsumoto, T.** 1954. Some doubtful Cretaceous ammonite genera from Japan and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **4:** 107–134, pls 7, 8.

—— **& Wright, E. V.** 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain. 40 pp. *Palaeontogr. Soc. (Monogr.)*, London.

Yabe, H. 1903. Cretaceous Cephalopoda from Hokkaido. Part 1. *J. Coll. Sci. imp. Univ. Tokyo* **18** (2): 1–55, pls 1–7.

Young, G. & Bird, J. 1828. *A geological survey of the Yorkshire coast.* 367 pp., 19 pls. Whitby.

Young, K. 1963. Upper Cretaceous ammonites of the Gulf Coast of the United States. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **6304:** 1–373, pls 1–82.

—— **& Powell, J. D.** 1978. Late Albian–Turonian correlations in Texas and Mexico. *Annls Mus. Hist. nat. Nice* **4** (XXV): 1–36, pls 1–9.

Zaborski, P. M. P. 1982. Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **36** (4): 303–332, 36 figs.

—— 1983. Campano-Maastrichtian ammonites, correlation and palaeogeography in Nigeria. *J. afr. Earth Sci.*, Oxford, **1:** 59–63.

Zittel, K. A. von 1884. Cephalopoda. *In: Handbuch der Palaeontologie*, **1** (Abt. 2, Lief. 3): 329–522. Munich and Leipzig.

—— 1895. *Grundzüge der Palaeontologie (Palaeozoologie).* vii+972 pp. Munich and Leipzig.

Note added in proof

Kennedy & Wright (1984) have recently reviewed the genus *Coilopoceras* and conclude that it is primarily a late Turonian form. They could find no good evidence for its occurrence before the middle Turonian. In view of their findings, it is possible that the uppermost exposed part of the Odukpani Formation in the Calabar region is somewhat younger than the early Turonian age suggested in this work.

Kennedy, W. J. & Wright, C. W. 1984. The Cretaceous ammonite *Ammonites requienianus* d'Orbigny, 1841. *Palaeontology*, London, **27:** 281–293, pls 35–37.

Index

New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

Aba 5*
Acanthoceras **33–9**
  alvaradoense 38; Zone 62*
  amphibolum 4, 34*, **35–8,** 36*, 37*, 39, 42, 51, 59–60; Zone 62*
  crassiornatum 33
  cunningtoni 42
    var. *cornuata* 38, 40
    var. *inermis* 40
  eschii 51
  eulessanum 42–3
  evolutum 40; aff. *evolutum* 40
  expansum 33
  flexuosum 33
  granerosense 59; Zone 62*; cf. *granerosense* 60
  haughi 30
  hazzardi 35
  hippocastanum 33
  jukesbrownei asssemblage 35; Zone 59, 62*
  latum 33
  lonsdalei 42
  meridionale 42
    var. *multicostata* 42
  muldoonense 51, 59–60; Zone 43, 62*
  munitum 33
  newboldi 31, 33
  quadratum 33
    nigeriense 58
  robustum 4, **33–5,** 34*, 59
  rhotomagense 33; Zone 59
    var. *sussexiense* 40, 59
  sussexiensis 40
  sp. 4, 37, **38–9**
Acanthocerataceae 22–58
Acanthoceratidae 26–53
Acanthoceratinae 33–9
Acompsoceras **29–30,** 58
  ansatramahaveloense 29
  calabarense 3, 27*, **29,** 31*
  catzigrasae 29
  essendiense 29, 58; aff. *essendiense* 3
  pseudosarthense 29
  renevieri 29–30; aff. *renevieri* 3, **30,** 31*, 58
  sahnii 29
  sarthense 29
  subwaterloti 29, 58
  tenue 29
  viotti 29
Afikpo 20
Africa 2
  north 42
  western 4, 42
Akanu 13
Akamkpa, see Calabar–Akamkpa road
Albian 3, 5*, 19, 58, 60–1
  Upper 3, 62*
Albian–Cenomanian boundary 58
Algeria 53, 61
Ammonites austeni 17
  bochumensis 29
  buddha 5
  cooperi 16
  cunningtoni 42, 45
  Egertoni 19
  egertonianus 19
  euomphalus 39
  harpax 30
  largilliertianus 22
  laticlavius 26
  lenticularis 57
  lobata 57
  meridionalis 42–3
  mitis 8
  neubergicus 19
  obtectus 22
  renevieri 30
  rhotomagensis 33, 40
  sacya 5, 7
  subobtectus 22
  sussexiensis 49
Anagaudryceras **5–8**
  buddha 7
  involvulum 4, 6*, **7–8,** 59
  mikobokense 8
  politissimum 8
  sacya 7
  utaturense 7
  yamashitai 8
Anaklinoceras 16; see *Nostoceras*
Anapuzosia 17; see *Puzosia*
Ancyloceras cheyennense 17
  lineatus 11, 13
  nebrascense 14
Angola 2, 7, 19, 26, 49, 59–60, 62*, 63; see also Barra do Dande, Luanda, Nova Redondo
Anisoceras cooperi 14, 16
Ariyalur Group 61
Atlantic Ocean, North 60
  South 4, 60
Austiniceras dibleyi 17, 19
Australasia 42
Awi Formation 3, 5*, 59, 62*

Baculites sp. 4
Barra do Dande fauna 62*
Benin Formation 3, 4*, 62*
Benue Valley 3, 61
Bostrychoceras 14, 61
  polyplocum Zone 61, 62*, 63
Brazil 22
British Museum (Natural History) 5, 63
Calabar, 2–3, 5, 5*, 7–8, 10–11, 13–14, 17, 19–20, 22, 24, 26, 32–3, 35, 38, 40, 43, 45, 49, 53, 55, 57, 59, 61, 62*, 63, 69
Calabar–Akamkpa road 3, 5*, 26, 29–30
Calabar–Ikot Ekpene road 3–5, 5*, 26, 29–30
Calycoceras 4, **32–3,** 58
  newboldi 33, 59; see also *Mantelliceras mantelli*
  (*Conlinoceras*) 32–3
    tarrantense Zone 59, 62*
  (*Newboldiceras*) **32–3**
    annulatum 4, **32–3,** 32*, 34*, 59–60
Cameroun 5*
Campanian 10, 13, 61
  late 63
  Lower 11, 13–14
  Upper 3, 4*, 10, 13–14, 17, 19, 61, 62*, 63
Cenomanian 2, 58, 60–1
  late 3, 26
  Lower 3, 26, 29–30, 33, 58, 61, 62*
  Middle 3, 7, 10–11, 19, 22, 24, 26, 32–3, 35, 38, 40, 43, 45, 49, 59–61, 62*
  Upper 30, 33, 60, 62*
Chalk 19
Christophoceras 13
  ramboulei 13
Cirroceras 14
Coahuilites 58
Coilopoceras **53–7,** 61, 69
  colleti 53, 61
  discoideum 57
  inflatum 57, 61
  newelli, 4, 55, 57, 61; aff. *newelli* 54*, **55–7,** 55*, 56*, 61
Coilopoceratidae 53–7
Colorado 43, 59, 60
Coniacian 10, 13, 61
Conlinoceras 32–3; see *Calycoceras*
Cordiceramus coxi 63; Zone 61
Cross River State Government 63
Cuanza Basin 60
Cunningtoniceras cunningtoni 42
  höltkeri 42
Cyphoceras 11; see *Pseudoxybeloceras*

Desmoceras latidorsatum 58
  sp. 3
  (*Pseudouhligella*) *calabarense* 58
    sp. 3
Desmocerataceae 17–22
Desmoceratidae 17–19

Dhondt, Dr A. 63
Didymoceras **14–17,** 61
  cheyennense 17, 61; aff. *cheyennense* 4, 15*, **17**
  fresnoense 17
  hornbyense 16, 61; aff. *hornbyense* 4, 12*, **14–17,** 15*
  kernense 16
  whiteavesi 14, 16
dimorphism 26, 57
dissolution 3, 58
Dukamaje Formation 63

Endocostea pteriodes 63
England 19, 26
  southern 35, 38, 58–60
Euhystrichoceras 58
  occidentale Zone 58
Euomphaloceras **39–51**
  asura 51
  cunningtoni 40, **42–51,** 59–60
    alatum 4, 43, **49–51,** 50*, 52*, 59
    cunningtoni 3, 38, 43, **45–9,** 46*, 47*, 51, 59–60
    lonsdalei 43, 60
    meridionale 3, 41*, 42, **42–5,** 44*, 48–9, 60
  cornutum 38, 52
  euomphalum 42
    var. *pervinquieri* 42
  inerme 3, **40,** 41*, 59–60
  lehmanni 51
  lonsdalei 42–3, 49
  meridionale 42–3
  multicostatum 51
  septemseriatum 3
Euomphaloceratinae 39–52
Europe 42
  north-west 20, 33, 60, 62*, 63
  western 59, 61
Exiteloceras bennisoni 17
  desertense 16
Eze-Aku Formation 61

folding 3, 5*, 59–61
Forbesiceras **22–6,** 58
  conlini 26; aff. *conlini* 58
  largilliertianum 26; aff. *largilliertianum* 26
  obtectum 3–4, **22–6,** 23*, 24*, 25*, 27*, 59–60
  sculptum 58
  subobtectum 3, **22,** 23*, 26
  sp. 3
Forbesiceratidae 22–6
France 40; see also Rouen, Normandy
  northern 59
  north-west 7, 26, 33, 59
  western 26

Gaudryceras **8–10**
  analabense 10
  beantalyense 4, **8–10,** 9*
  cinctum 10
  densiplicatum 8
  mite 8, 10
  propemite 10
  tenuiliratum 8
  varagurense 8
  varicostatum 4, **10,** 61
Gaudryceratidae 5–10
Glebosoceras 57
  glebosum 57
Gombe 63
Graneros Shale 59
Gulf of Guinea 63

Hamites clinensis 13
  vancouverensis 16
hardground 58
Haughiceras 30; see *Pseudocalycoceras*
Heteroceras Cheyennense 17
  hornbyense 14, 16
  perversum 16
Hokkaido 13
Hoplitoides crassicostatus 53
  ingens 57
Howarth, Dr M. K. 63
Hypoturrilites carcitanensis Zone 58

Ikot Ekpene 4*; see Calabar–Ikot Ekpene road
Ilorin, University of 5, 63
India 42, 61
  southern 7
inoceramid bivalves 63

Japan 38, 42, 59–60; see also Hokkaido

Kamerunoceras **51–3**
  tinrhertense 4, **51–3,** 52*, 54*, 61
  turoniense 53
Kennedy, Dr W. J. 63

Libycoceras 3, 63
  afikpoense 4, 63; Zone 61, 63
  crossense 4, 61, 63; Zone 63
  dandense 61, 63
  ismaelis 61
'Lower Limestone' 58
Luanda 60

Maastrichtian 13, 61–2
  early 63
  Lower 3, 4*, 8, 13, 20, 57, 61, 62*, 63
  Upper 61, 63
macroconch 26, 58
Malagasy Republic 10–11, 13, 42
Mantelliceras mantelli and *Calycoceras newboldi* Zone 33
  saxbii Zone 58
Mantelliceratinae 26–33
marine link 63
Metengonoceras dumbli 3
Metoicoeras 58
  geslinianum 60
  aff. *ornatum* 60
Mfamosing Quarry 3, 5*, 58–9
  Limestone Formation 58
microconch 26, 58
Middle East 42, 61
migration, faunal 60
Morocco 38
Morris, Dr N. J. 63
Mortoniceras 58

Neodesmoceras 10
New Zealand 10, 13
Newboldiceras 32; see *Calycoceras*
Nkporo Shale 3–4, 4*, 8, 10, 13–14, 17, 19–20, 57, 61, 62*, 63
Normandy 59
Nostoceras 4, 14, 16
  hornbyense 14
  mexicanum 16
  (*Anaklinoceras*) 16
Novo Redondo 26, 60; fauna 62*

Oban Massif 2
Odukpani Formation 3–4, 5*, 7, 10–11, 19, 22, 24, 26, 29–30, 32, 35, 38, 43, 45, 49, 53, 55, 57–61, 62*, 69

Pachydiscidae 19–22
Pachydiscus **19–22**
  dossantosi 4, 13, 18* **20–2,** 21*, 63
  egertoni 4, **19–20,** 21* 61
  egertonianus 19
  endymion 22
  gettyi 22
  gollevillensis 20, 22, 63
  jacquoti 22
  neubergicus 20, 22, 61; Zone 62*, 63
  stallauensis 20; aff. *stallauensis* 19–20
Pacific Coast, North America 13, 16, 61
Paracanthoceras amphibolum 35
Parapachydiscus dossantosi 20
  sp. 20
Parasolenoceras 11; see *Pseudoxybeloceras*
Peru 22, 55, 61
Phillips, D. 63
Phylloceras cf. *velledae* 58
Plesiacanthoceras amphibolum 35
  wyomingense 38
Polyaspidoceras 53
  shimizui 53
Precambrian 3, 62*
Pseudocalycoceras **30–2,** 61
  angolaense 31
  dentonense 31
  harpax 31
  haughi 30; cf. *haughi* 4, **30–2,** 31*, 60
  morpheus 31

paralouitense 31
(*Haughiceras*) *haughi* 30
Pseudouhligella, see *Desmoceras*
Pseudoxybeloceras 11–14
bicostatum 13
compressum 13
(*Cyphoceras*) 11, 13
nanaimoense 13
(*Parasolenoceras*) 11, 13, 61
bicostatum 14
clinensis 14
compressum 14
lineatum 14
nanaimoense 14
ramboulei 14
splendens 11, 13–14; aff. *splendens* 4, 12*, **13–14**
Puzosia **17–19**
buenaventura 17
matheroni 17
sp. 3–4, 58
(*Anapuzosia*) **17–19**
colusaensis 19
dibleyi 19; cf. *dibleyi* 3–4, **17–19,** 18*, 60
multicostata 19
saintoursi 19
Puzosiinae 17–19

Rouen 33, 35; fossil bed 26, 35, 40

Sahara 4, 53
Santonian 13, 61
Sciponoceras gracile faunal assemblage 60
Zone 61, 62*
Sharpeiceras 3, **26–9,** 58
congo 28
corroyi 28
falloti 28
florencae 28
goliath 28, 60
laticlavium **28–9,** 58, 60
nigeriense 3, 25*, **26–9,** 27*, 58
var. *indica* 29
var. *mexicanum* 29
occidentale 28
piveteaui 28
schlueteri 28
tlahualiloense 28
vohipalense 28
Solenoceras 11, 13
South Africa 10; see also Zululand
Sphenodiscidae **57–8**
Sphenodiscus 3, 13, **57–8,** 63
lobatus 61
costatus 4, 56*, **57–8**
lobatus 4
pleurisepta 58
studeri 63; Zone 61

Taylor Formation 13
Tertiary, see Benin Formation
Tethys 63
Tetragonitaceae 5–10
Texas 13, 26, 38, 43, 60
Thatcher Limestone Member 59
Trochoceramus radiosus 63
Turrilitaceae 10–17
Turrilites **10–11**
acutus 4, **11,** 59–60; assemblage 35; Zone 35, 59–60, 62*
costatus 3, **10–11,** 12*, 58–60; Zone 33, 58–60, 62
scheuchzerianus 3, 7*, **10,** 11, 12*, 59; Zone 58
Turrilitidae 10–17
Turrilitinae 10–11
Turonian 3, 55, 57, 59, 61
early 3, 69
mid 61, 69
late 61, 69
Lower 5*, 53, 55, 60–1, 62*

unconformity 3, 60–1
United States 22, 42, 61; see also Texas, Colorado
western interior 38, 43, 57, 59, 61, 62*, 63

Wright, Dr C. W. 63

Zululand 33, 35

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British Museum (Natural History)

The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

B. G. Gardiner

There are some 25,000 species of actinopterygians, far out-numbering the tetrapods and accounting for over half of all the living species of vertebrates. The Actinopterygii contain such diverse forms as polypterids, sturgeons, paddle fishes, gars, the bowfin and the enormous variety of teleosts. The Devonian actinopterygians described in this monograph stand near the base of the Osteichthyes, a natural group including the coelacanths, lungfishes and tetrapods.

This unique Upper Devonian fish fauna was discovered in 1963 by Mr Harry Toombs of the British Museum (Natural History) while on a collecting trip to Australia. The majority of the material was subsequently collected in 1967 by a joint expedition from the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow.

The discovery of these superbly preserved Devonian palaeoniscids at Gogo, Western Australia, has not only greatly increased our knowledge of the early actinopterygian condition but has also enabled us to appreciate the original osteichthyan plan. In other words, many of the characters of the Gogo palaeoniscids are primitive for all bony fishes, and this in turn allows comparison with the other gnathostome groups. These Devonian species also provide detailed information which illuminates many problems in the structure and evolution of the actinopterygians. This knowledge has permitted a more comprehensive and soundly based account of the history of that group.

The relationships are expressed in a new classification of gnathostomes in which the placoderms are considered to be the sister-group of the osteichthyans, the acanthodians the sister-group of those two and the chondrichthyans the primitive sister-group of other gnathostomes. The Porolepiformes are considered to be the sister-group of the choanates.

Finally the interrelationships of actinopterygians are reviewed and the great range of fossil forms presently included in the Palaeonisciformes discussed.

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Cenomanian and Turonian ammonites from the Novo Redondo area, Angola

M. K. Howarth

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M. K. Howarth

Department of Palaeontology, British Museum (Natural History), Cromwell Road,
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Contents

Synopsis ... 74
Introduction ... 74
Localities, faunas and ages ...
  Lower Cenomanian ... 76
  Localities of probable Lower Cenomanian age ... 76
  Middle Cenomanian ... 77
  Upper Cenomanian and Lower Turonian ... 77
Systematic descriptions ... 78
 Family Phylloceratidae Zittel ... 78
  Genus *Phylloceras* Suess ... 78
   Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière ... 79
 Family Turrilitidae Gill ... 79
  Genus *Ostlingoceras* Hyatt ... 79
   Ostlingoceras (*O.*) cf. *rorayense* (Collignon) ... 79
  Genus *Mariella* Nowak ... 79
   Mariella (*M.*) *oehlerti* (Pervinquière) ... 79
  Genus *Turrilites* Lamarck ... 81
   Turrilites (*T.*) *acutus* Passy ... 81
 Family Desmoceratidae Zittel ... 82
  Genus *Desmoceras* Zittel ... 82
   Desmoceras (*D.*) *latidorsatum lemoinei* Collignon ... 82
 Family Placenticeratidae Hyatt ... 84
  Genus *Proplacenticeras* Spath ... 84
   Proplacenticeras stantoni (Hyatt) var. *bolli* (Hyatt) ... 84
 Family Forbesiceratidae Wright ... 85
  Genus *Forbesiceras* Kossmat ... 85
   Forbesiceras obtectum (Sharpe) ... 86
 Family Acanthoceratidae Grossouvre ... 86
  Genus *Sharpeiceras* Hyatt ... 86
   Sharpeiceras florencae Spath ... 86
   Sharpeiceras mexicanum (Böse) ... 88
  Genus *Calycoceras* Hyatt ... 91
   Calycoceras (*C.*) *naviculare* (Mantell) ... 91
  Genus *Euomphaloceras* Spath ... 93
   Euomphaloceras (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka) ... 93
   Euomphaloceras (*Kanabiceras*) *septemseriatum* (Cragin) ... 95
  Genus *Pseudaspidoceras* Hyatt ... 97
   Pseudaspidoceras footeanum (Stoliczka) ... 98
 Family Vascoceratidae Douvillé ... 100
  Genus *Vascoceras* Choffat ... 100
   Vascoceras (*Paravascoceras*) *harttii* (Hyatt) ... 100
References ... 101
Index ... 104

Bull. Br. Mus. nat. Hist. (Geol.) **39** (2): 73–105

Issued 29 August 1985

Synopsis

About one hundred ammonites collected from 24 localities near Novo Redondo indicate various dates in the Cenomanian and Lower Turonian. The Lower Cenomanian ammonites include large examples of *Sharpeiceras*, especially *S. florencae*, and also many specimens of *Desmoceras latidorsatum lemoinei*, and species of *Ostlingoceras* and *Mariella*. Middle Cenomanian ammonites include large specimens of *Euomphaloceras* (*E.*) *cunningtoni* and *Forbesiceras obtectum*. One locality has a mixture of the Upper Cenomanian ammonites *Calycoceras naviculare* and *Euomphaloceras* (*Kanabiceras*) *septemseriatum*, and the Lower Turonian ammonites *Pseudaspidoceras footeanum, Vascoceras* (*Paravascoceras*) *harttii* and *Proplacenticeras stantoni*. These are the first records of ammonites in Angola referable to the middle part of the Lower Turonian.

Introduction

The rich ammonite faunas from the Cretaceous rocks of the coastal regions of Angola have been described by many authors. All the stages from the Albian to the top of the Cretaceous contain ammonites, and an earlier review of the faunas by Howarth (1965: 340–343, 400–405), was followed by an up-to-date review of the biostratigraphy of the Albian to Turonian stages by Cooper (1978*b*). Novo Redondo is about 270 km south of Luanda, and lies in the southern half of the Cuanza sedimentary basin. Lower and Middle Cenomanian ammonites from the surrounding district were described by Cooper (1973), and included notable examples of the genera *Turrilites, Euomphaloceras* and *Forbesiceras*. The new collection of about 100 ammonites described here includes more examples of these three genera, together with a fauna of large specimens of the Lower Cenomanian genus *Sharpeiceras*, of which only one Angolan specimen has been described and figured before (Haas 1942). Also included is a small number of ammonites from a locality a short distance south of Novo Redondo that contains species of both Upper Cenomanian and Lower Turonian age. The latter species are slightly younger than the basal Turonian ammonites of Salinas, revised by Cooper (1978*a*), and older than the mid-Turonian ammonites of Moçamedes that were described by Howarth (1968); they fill an age gap that has not hitherto been represented by ammonites in Angola.

The collecting localities, which are shown in Fig. 1, all lie within sheet 184, Novo Redondo, of the 1:100000 geological survey maps of Angola (Lapao 1972). In fact the localities lie between 10 km south and 25 km NNE of Novo Redondo, and can be readily plotted on the detailed geological map of sheet 184; Fig. 1 outlines the geological relationships in the area. Pre-Cambrian basement rocks to the east are overlain by Cretaceous rocks in a coastal strip, here 25–30 km wide, which start with non-marine Aptian sediments, overlain by marine Albian, Cenomanian, and some representatives of other stages, up to the top of the Cretaceous. The total thickness of the Cretaceous is 700–1000 m. More details of the stratigraphy within each stage, and the ammonites from which the age had been determined, were given by Lapao (1972: 10–32), but no details are available of the stratigraphy at each ammonite locality. They appear to represent single dates, except for the mixture of Upper Cenomanian and Lower Turonian ammonites at locality 1007.

North of Novo Redondo the Lower Cenomanian is shown separately on Lapao's map (1972), but the area it occupies does not entirely accord with the ages given by the ammonites at some localities. Localities 67, 72 and 76 near the northern edge of the map contain the Lower Cenomanian ammonite *Sharpeiceras*, but they occur within the area shown on the map as Middle/Upper Cenomanian. A few km south of Novo Redondo the facies becomes somewhat different and the Cenomanian is not divided. No divisions within the Cenomanian are shown on the sketch map of Fig. 1: instead, the Lower or Middle Cenomanian dates suggested by the ammonites are shown by lettering on appropriate areas of the map. It can be seen that all the localities north of Novo Redondo are Lower Cenomanian, while those south of Novo Redondo are mainly Middle Cenomanian in age.

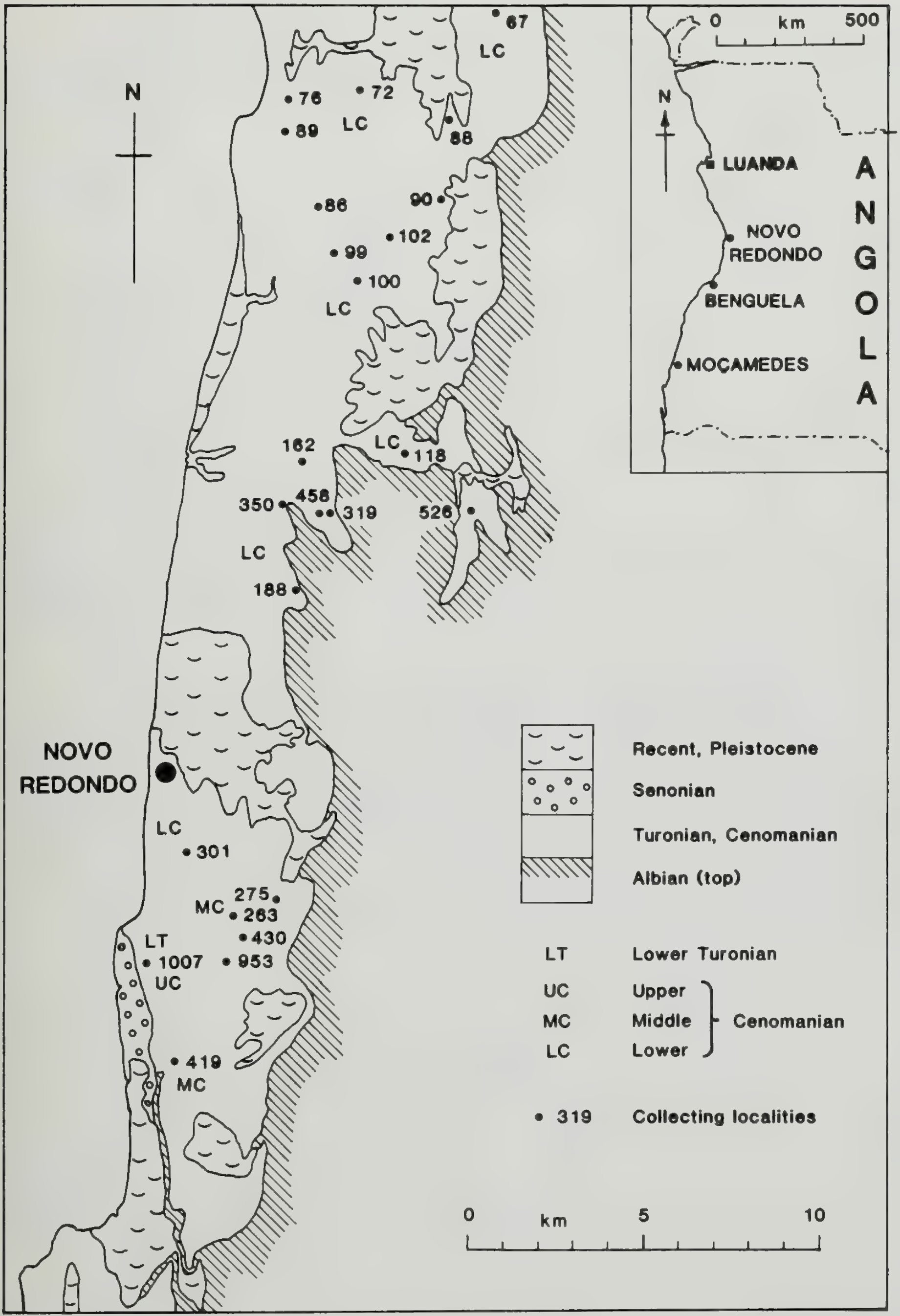

N
67
LC
76
72
89
LC
88
86
90
102
99
100
LC
162
LC
118
350
458
319
526
LC
188
NOVO
REDONDO
LC
301
MC
275
263
430
LT
1007
953
UC
419
MC
0 km 500
N
LUANDA
NOVO
REDONDO
BENGUELA
MOÇAMEDES
ANGOLA
Recent, Pleistocene
Senonian
Turonian, Cenomanian
Albian (top)
LT Lower Turonian
UC Upper
MC Middle
LC Lower
Cenomanian
319 Collecting localities
0 km 5 10

Fig. 1 Map of the collecting localities and an outline of the geology in the area around Novo Redondo, Angola.

Localities, faunas and ages

Lower Cenomanian

Localities 67, 23·5 km NNE of Novo Redondo; 72, 20 km NNE of Novo Redondo; 100, 15 km NNE of Novo Redondo; 188, 6 km NE of Novo Redondo; and 526, 11·5 km NE of Novo Redondo
Sharpeiceras florencae Spath

Locality 76, 19·5 km north of Novo Redondo
Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière
Sharpeiceras florencae Spath
Puzosia sp. indet.

Localities 86, 16·5 km NNE of Novo Redondo; and 118, 11·5 km NE of Novo Redondo
Desmoceras (*D.*) *latidorsatum lemoinei* Collignon
Puzosia sp. indet.

Locality 88, 20 km NNE of Novo Redondo
Desmoceras (*D.*) *latidorsatum lemoinei* Collignon
Sharpeiceras florencae Spath
Puzosia sp. indet.

Locality 90, 18 km NNE of Novo Redondo
Sharpeiceras mexicanum (Böse)

Localities 99, 15·5 km NNE of Novo Redondo; and 102, 16·5 km NNE of Novo Redondo
Sharpeiceras florencae Spath
S. mexicanum (Böse)

Locality 301, 2·5 km SSE of Novo Redondo
Ostlingoceras (*O.*) cf. *rorayense* (Collignon)

Locality 350, 8·5 km NNE of Novo Redondo
Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière
Mariella (*M.*) *oehlerti* (Pervinquière)
Desmoceras (*D.*) *latidorsatum lemoinei* Collignon

Locality 458, 8·5 km NNE of Novo Redondo
Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière
Desmoceras (*D.*) *latidorsatum lemoinei* Collignon
Gaudryceras sp. indet.

Most of the genera and species found at these localities are accurate indicators of a Lower Cenomanian age. *Sharpeiceras* is probably confined to the Lower Cenomanian, and *S. florencae* occurs in the Carcitanensis Zone in England, the basal zone of the Cenomanian in the scheme adopted by Kennedy & Hancock (1978: V.14). The subspecies *Desmoceras latidorsatum lemoinei* is characteristic of the Lower Cenomanian, as are also the two Turrilitidae species *Ostlingoceras* (*O.*) *rorayense* and *Mariella* (*M.*) *oehlerti*. Therefore a Lower Cenomanian age is applicable to all 15 localities listed above. The *Puzosia* sp. indet. recorded at localities 76, 86 and 88, and the *Gaudryceras* sp. indet. at locality 458, are based on poorly-preserved fragmentary specimens that are not specifically identifiable; they are not described in the systematic section of the paper.

Localities of probable Lower Cenomanian age

Locality 89, 18·5 km north of Novo Redondo
Gaudryceras sp. indet.

Localities 162, 9·5 km NNE of Novo Redondo; and 319, 8·5 km NNE of Novo Redondo
Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière

These three localities can be dated as Cenomanian, and probably Lower Cenomanian, by their proximity to other localities that are definitely dated as Lower Cenomanian (localities 89 and 162 are near to 76 and 350 respectively), and both the ammonites are associated with Lower Cenomanian species at other localities.

Middle Cenomanian

Locality 263, 4·5 km SE of Novo Redondo
Euomphaloceras (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka)

Locality 275, 5 km SE of Novo Redondo
Forbesiceras obtectum (Sharpe)
E. (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka)

Locality 419, 8 km south of Novo Redondo
Turrilites (*T.*) *acutus* Passy
Forbesiceras obtectum (Sharpe)

Locality 430, 5 km SE of Novo Redondo
E. (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka)

Locality 953, 6 km SE of Novo Redondo
Turrilites (*T.*) *acutus* Passy
Forbesiceras obtectum (Sharpe)
E. (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka)

Only three species of ammonites occur at these five localities, but the presence of all three together at locality 953 suggests that all five localities are of approximately the same age. The most accurate indicator of that age is probably *Turrilites* (*T.*) *acutus*, which occurs most commonly in the Acutus Zone, the middle one of the three zones of the Middle Cenomanian in north-west Europe (Kennedy 1971: 102; Kennedy & Hancock 1978: V.15). The genus *Euomphaloceras* first appeared in the Middle Cenomanian, and *E. cunningtoni* occurs in the Acutus Zone, though it is more abundant in the underlying Costatus Zone (Kennedy 1971: 90, 102). *Forbesiceras obtectum* also occurs in the Acutus Zone, and well as at lower levels in the Middle and the top of the Lower Cenomanian (Kennedy 1971: 48, 102). If a single age can be assigned to these five localities, it is most probably *Turrilites acutus* Zone, Middle Cenomanian. The underlying *Turrilites costatus* Zone is a less likely possibility.

Upper Cenomanian and Lower Turonian

Locality 1007, 5·5 km south of Novo Redondo
Proplacenticeras stantoni (Hyatt) var. *bolli* (Hyatt)
Calycoceras (*C.*) *naviculare* (Mantell)
Euomphaloceras (*Kanabiceras*) *septemseriatum* (Cragin)
Pseudaspidoceras footeanum (Stoliczka)
Vascoceras (*Paravascoceras*) *harttii* (Hyatt)

Both Upper Cenomanian and Lower Turonian strata are present at this locality. *Calycoceras naviculare* occurs in the Naviculare Zone and in the overlying Geslinianum Zone of the Upper Cenomanian, but neither it nor the genus *Calycoceras* go higher than the top of the Cenomanian (Wright & Kennedy 1981: 33). *Euomphaloceras septemseriatum* is characteristic of the Geslinianum Zone and is probably confined to that horizon. These two species indicate the presence of at least the Geslinianum Zone of the Upper Cenomanian, but there is no evidence for the uppermost zone of the Cenomanian, i.e. the Juddii Zone, in the scheme adopted by Wright & Kennedy (1981: 8). Of the other three species, *Pseudaspidoceras footeanum* is the clearest indicator of a Lower Turonian age, because the genus does not occur below the Turonian, and *P. footeanum* itself occurs in the Lower Turonian of Israel (Freund & Raab 1969: 14, 73), England (Wright & Kennedy 1981: 82) and southern India. The genus *Vascoceras* first appears in the Geslinianum Zone, Upper Cenomanian, but it is more characteristic of the Turonian, and *V.* (*Paravascoceras*) *harttii* is similar to species that occur near the top of the Lower Turonian in Portugal (see p. 101). Species of *Proplacenticeras* first occur in the Upper Cenomanian, Geslinianum Zone of Europe (Wright & Kennedy 1981: 123), but *P. stantoni* var. *bolli* is nearly identical to specimens that are found in the Lower Turonian Britton Formation in Texas (Moreman 1942: 192, Young & Powell 1978: XXV.18). So the evidence of the ammonites at locality 1007 suggests that beds of both Upper Cenomanian, Geslinianum Zone, and Lower Turonian age are present.

Systematic descriptions

All the specimens are in the collections of the British Museum (Natural History) and catalogue numbers have the prefix letter C. Measurements are given in the order diameter (D), whorl height (Wh), whorl breadth (Wb), diameter of the umbilicus (U), and figures in brackets are proportions of the diameter.

Suborder **PHYLLOCERATINA** Arkell, 1950

Family **PHYLLOCERATIDAE** Zittel, 1884

Genus ***PHYLLOCERAS*** Suess, 1865

Subgenus ***HYPOPHYLLOCERAS*** Salfeld, 1924

TYPE SPECIES. *Phylloceras onoense* Stanton, 1895.

Phylloceras* (*Hypophylloceras*) *seresitense Pervinquière
Fig. 2

1907 *Phylloceras velledae* var. *seresitense* Pervinquière: 52.
1910 *Phylloceras velledae* var. *seresitense* Pervinquière; Pervinquière: 9; text-fig. 2; pl. 1, figs 1–3.
1977 *Phylloceras* (*Hypophylloceras*) *seresitense* Pervinquière; Kennedy & Klinger: 363–365; pl. 4, figs 6, 7; pl. 6, fig. 4; pl. 7, fig. 4; pl. 9.
1978 *Phylloceras* (*Hyporbulites*) *seresitense seresitense* Pervinquière; Collignon: 2; pl. 1, fig. 1.
1979 *Phylloceras* (*Hypophylloceras*) *seresitense* Pervinquière; Cooper & Kennedy: 177–181; figs 1, 2, 3I (q.v. for full synonymy).

MATERIAL. Six specimens, C.80994–5 (loc. 76), C.81010 (loc. 162), C.81020 (loc. 319), C.81034 (loc. 350) and C.81046 (loc. 458).

MEASUREMENTS.	D	Wh	Wb	Wb:Wh
C.80995	136	81·6 (0·60)	39·3 (0·29)	0·48
C.80994	—	70·3	37·5	0·53

REMARKS. The best specimen is the half ammonite, 136 mm in diameter, figured in Fig. 2. C.80994 is a quarter-whorl fragment of similar size, and the remaining four are much smaller fragments. They are referred to *P.* (*H.*) *seresitense* on the basis of their general whorl proportions, the slightly flexuous striate ornament, and the tetraphylloid saddle endings of the suture lines. The umbilicus appears to be nearly or completely closed, and low, slightly flexuous constrictions can be seen on the figured specimen.

This species has been fully discussed by Kennedy & Klinger (1977) and Cooper & Kennedy (1979), and in the latter paper specimens from the Upper Albian of Angola were described and figured. A small example from the Upper Albian was also figured by Collignon (1978: pl. 1, fig. 1). The specimens now described extend the range of the species in Angola up into at least the Lower Cenomanian. Many European examples were described in three papers by Wiedmann (1962*a*, 1962*b*, 1964), who divided the species into three subspecies according to the degree of compression of the whorls and the size of the umbilicus. Cooper & Kennedy (1979: 180; fig. 2) found considerable variation in whorl compression, and did not accept that the subspecies divisions were valid. This view seems to be supported by the present few specimens which have whorl breadth/height ratios of 0·48 and 0·53 at about 120–135 mm diameter, and agree with Cooper & Kennedy's (1979: 181; fig. 2) graph of whorl dimensions extrapolated to slightly larger diameters.

OCCURRENCE. This species ranges from the Upper Aptian to the middle of the Cenomanian.

Suborder **ANCYLOCERATINA** Wiedmann, 1960

Superfamily **TURRILITACEAE** Gill, 1871

Family **TURRILITIDAE** Gill, 1871

Genus ***OSTLINGOCERAS*** Hyatt, 1900

TYPE SPECIES. *Turrilites puzosianus* d'Orbigny, 1842.

Ostlingoceras* (*Ostlingoceras*)** cf. ***rorayense (Collignon)

Fig. 5

1964 *Turrilites rorayensis* Collignon: 49; pl. 330, fig. 1479.
1975 *Ostlingoceras* (*O.*) *rorayense* (Collignon); Förster: 186; pl. 6, figs 7, 8.
1978 *Ostlingoceras* (*O.*) *rorayense* (Collignon); Klinger & Kennedy: 11; pl. 1, figs M, N; pl. 5, fig. G; pl. 8, fig. E.

MATERIAL. One specimen, C.81019, from loc. 301.

REMARKS. This is a fragment, only 13 mm high, of three small whorls that are sinistrally coiled, have a small apical angle, and almost flat sides to the whorl. The ornament consists of weak ribs just below the upper whorl suture which end in a row of tubercles about the middle of the flank, then a narrow smooth band down to the second row of tubercles just above the lower whorl suture. A third row of tubercles is not visible, but could be hidden by the overlap of the whorls.

The close coiling, low apical angle, flat sides, weak ribs and small tubercles suggest that this small fragment belongs to the subgenus *Ostlingoceras*, and comparison is made with Collignon's species which has been revised by Klinger & Kennedy (1978) on the basis of more than 150 specimens from the Lower Cenomanian of Zululand.

OCCURRENCE. The Lower Cenomanian of Madagascar, Mozambique, Zululand and Angola.

Genus ***MARIELLA*** Nowak, 1916

TYPE SPECIES. *Turrilites bergeri* Brongniart, 1822.

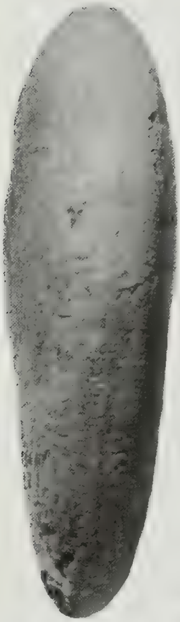
Mariella* (*Mariella*) *oehlerti (Pervinquière)

Figs 4, 6

1907 *Turrilites gresslyi* Pictet & Campiche; Boule, Lemoine & Thévenin: 57; pl. 13, fig. 2.
1910 *Turrilites oehlerti* Pervinquière: 53; pl. 5, figs 14–17.
1929 *Turrilites gresslyi* Pictet & Campiche; Collignon: 41; pl. 6, fig. 15.
1929 *Turrilites oehlerti* Pervinquière; Collignon: 41; pl. 6, figs 16, 17.
1964 *Turrilites oehlerti* Pervinquière; Collignon: 15; pl. 320, figs 1398, 1399.
1978 *Mariella* (*M.*) *oehlerti oehlerti* (Pervinquière) Klinger & Kennedy: 31; pl. 3, fig. E; pl. 4, fig. E; pl. 6, figs H–N; pl. 7, fig. G; pl. 8, figs G, H.

MATERIAL. Three specimens, C.81035–7, from loc. 350.

DESCRIPTION. The collection consists of one fragment of half a large whorl of about 55 mm diameter, and two small fragments showing parts of two and three whorls respectively from about 6 to 25 mm diameter. All are coiled sinistrally. The whorl of the larger specimen has a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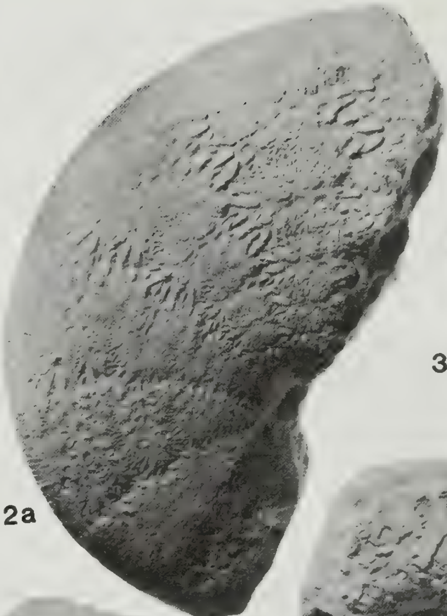
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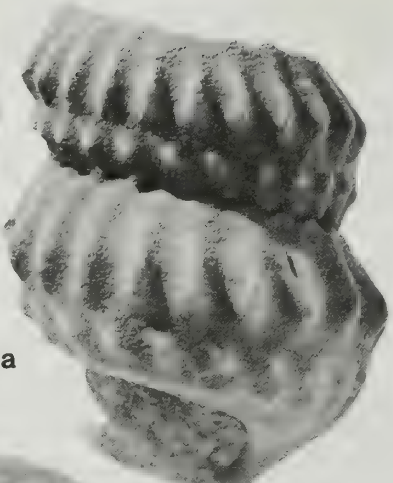
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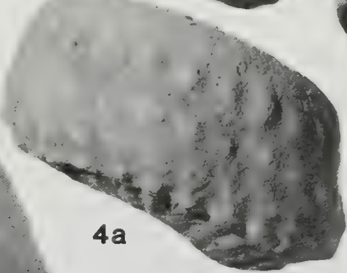
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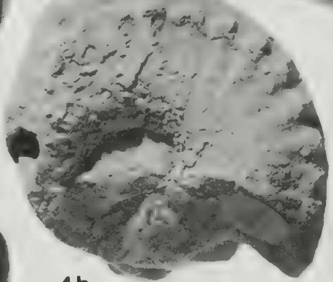
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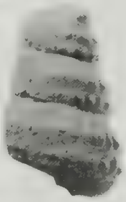
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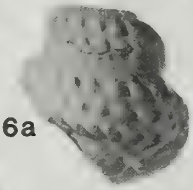
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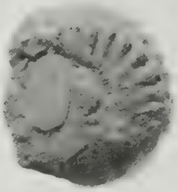
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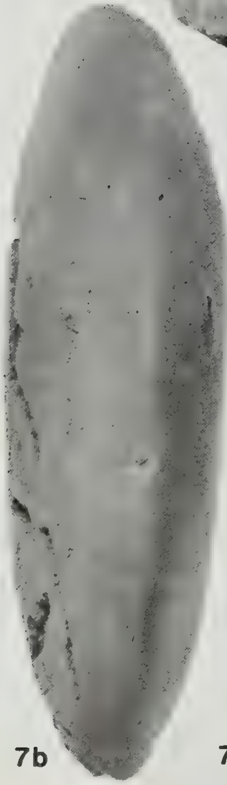
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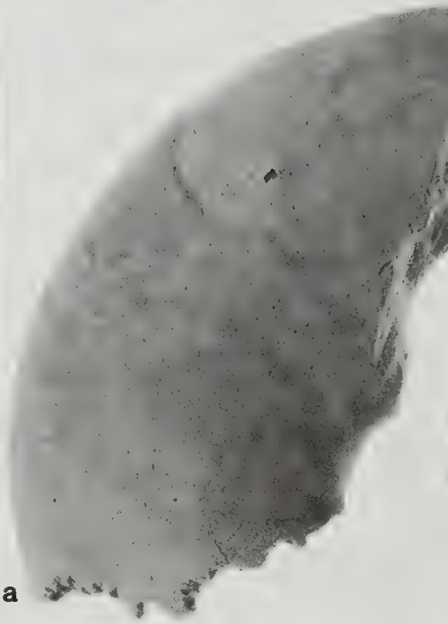
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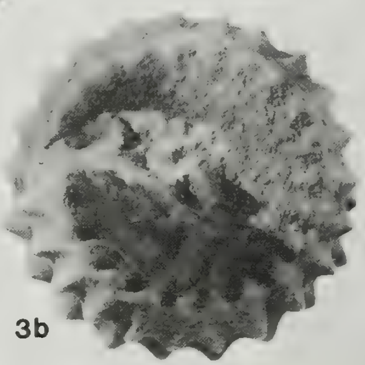
3b

flattened outer side and is angled at the upper whorl suture but more rounded at the lower one. The smaller specimens have more rounded whorls. The main ornament consists of four rows of tubercles, the upper row just above the middle of the whorl, the next row just below the middle of the whorl, and the two lowest rows much closer to each other and near the lower whorl suture. The lowest row is usually hidden by the overlap of the next larger whorl. There is an equal number of tubercles in each row, aligned obliquely in the direction of the spire. The tubercles in the lowest row are smaller than the others. The tubercle density is about 15 per half whorl in the larger fragment and about 12 per half whorl in the smaller ones. Bands between the tubercles and up to the upper whorl suture are smooth, and ribs are only weakly developed on the bottom of the whorl in the zone of overlap. No suture-lines are visible.

REMARKS. These specimens are not sufficiently well preserved to show whether they belong to the nominate subspecies or to the subspecies *sulcata* of Klinger & Kennedy (1978: 33; pl. 3, fig. D; pl. 8, fig. D). The latter differs from the nominate subspecies in having a spiral groove between the second and third rows of tubercles. Such a groove is not present in these Angolan examples, although there appears to be a groove between the top and second rows in the largest specimen which might be a preservational feature. All the morphological features that can be seen, including the density of tubercles, match those of Pervinquière's species, which was revised by Klinger & Kennedy (1978) on the basis of several hundred specimens from Zululand.

OCCURRENCE. The Lower Cenomanian of north Africa, Angola, Zululand and Madagascar.

Genus ***TURRILITES*** Lamarck, 1801

TYPE SPECIES. *Turrilites costatus* Lamarck, 1801.

Turrilites (Turrilites) acutus Passy
Fig. 3

1832 *Turrilites acutus* Passy: 7; pl. 16, figs 3, 4.
1973 *Turrilites (Turrilites) acutus* Passy; Cooper: 47; figs 2D, 3A–C, 8D, 13B.
1978 *Turrilites (T.) acutus* Passy; Klinger & Kennedy: 7; pl. 2, figs A–E.

MATERIAL. Three specimens, C.81040–1 from loc. 419, and C.81067 from loc. 953.

DESCRIPTION. Each of the three large specimens consists of parts of two sinistrally coiled whorls up to 50–60 mm diameter. They are preserved mainly as internal moulds, though no suture-lines can be seen. Three rows of prominent tubercles form the main ornament, an upper row of large, pointed tubercles just above the middle of the whorl, a row of smaller pointed tubercles on the bottom half of the whorl, and a row of small tubercles that are just exposed above the lower whorl suture. There are approximately equal numbers of tubercles in each row. Those in the middle and upper rows are elongated obliquely to form weak ribs between the rows and stronger ribs that reach nearly up to the upper whorl suture.

REMARKS. Several closely similar specimens from the Middle Cenomanian at nearby localities south of Novo Redondo were described and figured by Cooper (1973: 47), and the species has been described by Klinger & Kennedy (1978: 7) on the basis of a large number of specimens

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Fig. 2 *Phylloceras (Hypophylloceras) seresitense* Pervinquière from Lower Cenomanian at loc. 76. C.80995, ×0·65.

Fig. 3 *Turrilites (T.) acutus* Passy from Middle Cenomanian at loc. 419; Fig. 3b is the top of the spire. C.81040, ×1.

Figs 4, 6 *Mariella (M.) oehlerti* (Pervinquière) from Lower Cenomanian at loc. 350; Figs 4b and 6b are the bases of the spires. Fig. 4, C.81037, ×1. Fig. 6, C.81035, ×1.

Fig. 5 *Ostlingòceras (O.)* cf. *rorayense* (Collignon) from Lower Cenomanian at loc. 301. C.81019, ×2.

Fig. 7 *Proplacenticeras stantoni* (Hyatt) var. *bolli* (Hyatt) from Lower Turonian at loc. 1007. C.81058, ×0·67.

from the Middle Cenomanian of Zululand. A full synonymy can be found in the latter paper. The three specimens described here agree in all characters, and show that at these large sizes the tubercles in the lowest row are exposed just above the next larger whorl.

OCCURRENCE. Middle and low Upper Cenomanian of Europe, Africa, Madagascar and North America.

Suborder **AMMONITINA** Hyatt, 1889

Superfamily **DESMOCERATACEAE** Zittel, 1895

Family **DESMOCERATIDAE** Zittel, 1895

Genus ***DESMOCERAS*** Zittel, 1884

TYPE SPECIES. *Ammonites latidorsatus* Michelin, 1836.

Desmoceras* (*Desmoceras*) *latidorsatum lemoinei Collignon
Figs 8–13

1928 *Desmoceras* (*Latidorsella*) *latidorsata* (Michelin); Collignon: 157; pl. 2, figs 4, 5.
1928 *Desmoceras* (*Latidorsella*) *lemoinei* Collignon: 158; pl. 2, fig. 6.
1942 *Desmoceras kossmati* Matsumoto: 26; fig. 12.
1954 *Desmoceras kossmati* Matsumoto; Matsumoto: 249; pl. 1, figs 1–6; pl. 6, fig. 6.
? 1958 *Desmoceras* (*Pseudouhligella*) *elgini* Young: 292; pl. 39, figs 4–20, 24–5, 30–1.
1959 *Desmoceras kossmati* Matsumoto; Matsumoto: 7; pl. 2, fig. 2.
1984 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin); Wright & Kennedy: 61; pl. 3, figs 3, 5, 7–8, 13.

MATERIAL. Twenty-two specimens, C.80982–6 (loc. 86), C.80996–7 (loc. 88), C.81008 (loc. 118), C.81021–33 (loc. 350) and C.81045 (loc. 458).

MEASUREMENTS.	D	Wh	Wb	N	Wh:Wb
C.80982	55·5	25·2 (0·45)	25·4 (0·46)	14·0 (0·25)	0·99
C.80983	34·5	17·5 (0·51)	17·2 (0·50)	7·3 (0·21)	1·02
C.81023	24·8	12·0 (0·48)	10·6 (0·43)	5·1 (0·21)	1·13
C.81024	34·0	15·4 (0·45)	17·4 (0·51)	8·5 (0·25)	0·88
C.81025	26·0	11·9 (0·46)	14·5 (0·55)	6·0 (0·23)	0·82

DESCRIPTION. The 22 specimens range in size from 66 mm diameter down to 13 mm. Body chambers are preserved in nearly half of them, and are of all sizes (therefore many are immature specimens), while septa are present in one specimen up to a diameter of 44 mm. None have a complete adult mouth border preserved. The whorl shape is subcircular, with flattish sides, an evenly rounded venter, and rounded umbilical edges. The whorl proportions vary from slightly depressed to slightly compressed (whorl height/breadth ratios from 0·88 to 1·13). The shell surface is smooth and unornamented, apart from curved or biconcave constrictions which are irregularly developed in some specimens from sizes at least as small as 13 mm diameter. These constrictions are projected well forwards on the venter, where they are usually accompanied by a raised collar immediately behind.

REMARKS. Collections of *Desmoceras latidorsatum* (Michelin) show much variation in whorl proportions and shape and strength of constrictions, as was described by Wiedmann & Dieni (1968: 131) and Cooper & Kennedy (1979: 239). The nominal species is of Middle Albian age,

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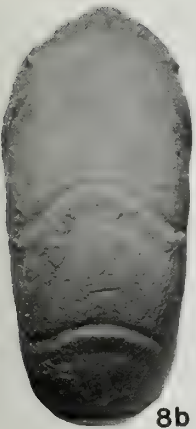
Figs 8–13 *Desmoceras* (*D.*) *latidorsatum lemoinei* Collignon from Lower Cenomanian. Figs 8, 12, 13 from loc. 86; Figs 9–11 from loc. 350. All ×1. Fig. 8, C.80982; Fig. 9, C.81025; Fig. 10, C.81023; Fig. 11, C.81024; Fig. 12, C.80983; Fig. 13, C.80981.

Fig. 14 *Forbesiceras obtectum* (Sharpe) from Middle Cenomanian at loc. 419. C.81078, ×0·6.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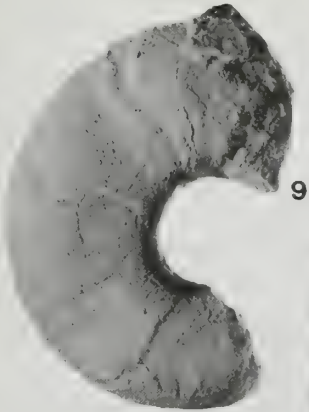
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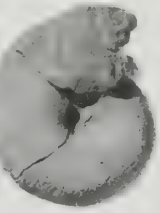
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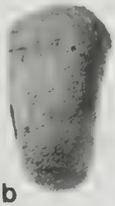
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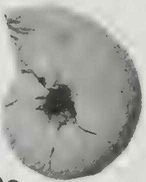
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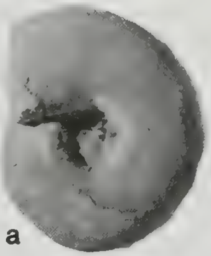
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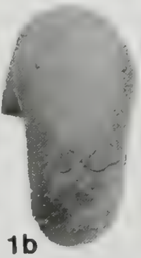
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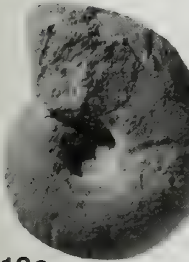
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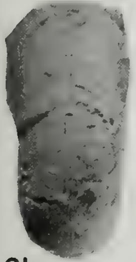
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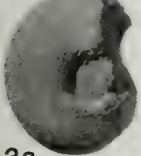
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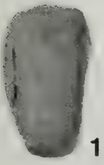
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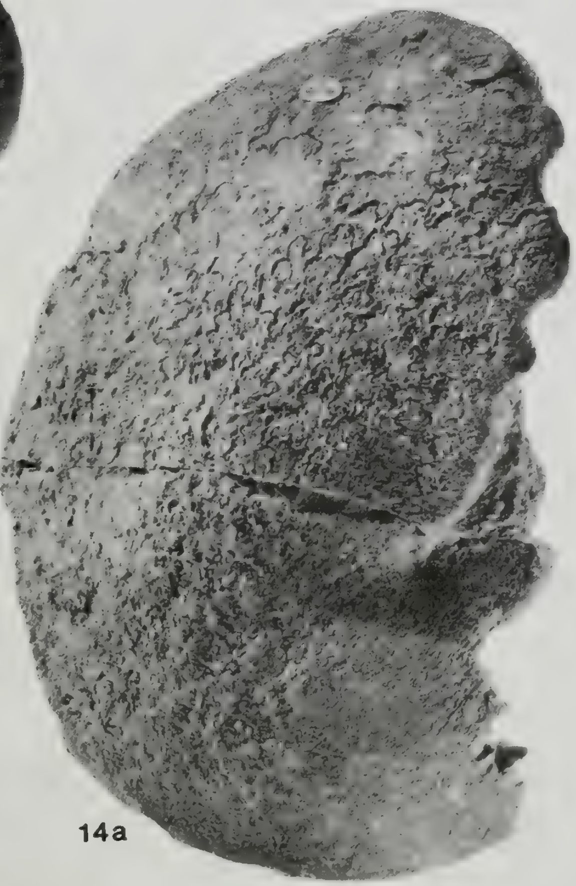
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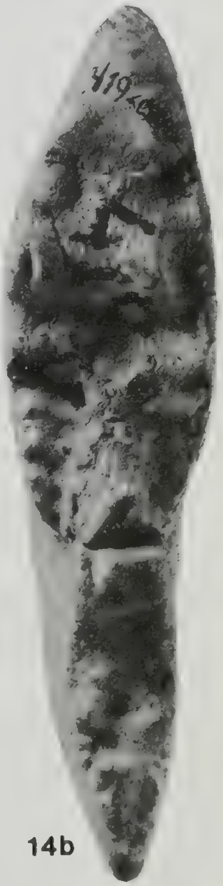
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and the overall morphological change in collections from younger horizons is considered sufficient to give subspecific names to them. Those in the uppermost Albian of Angola are more depressed and have been called *Desmoceras latidorsatum perinflatum* Cooper & Kennedy (1979: 237), although the correct name for this subspecies appears to be *D. latidorsatum inflatum* Breistroffer (1933) or *D. latidorsatum reynesianum* Haas (1952) according to their synonymy. In the Lower Cenomanian species that are now described, the whorls have become slightly more compressed again, so that all the measurable ones fall below the scatter of points of the Upper Albian specimens on Cooper & Kennedy's graph (1979: 240, fig. 38, upper). They also differ from the Middle Albian subspecies in having weaker and fewer constrictions. The slight morphological shift in these features is sufficient for them to be referred to a different chronological subspecies, for which *lemoinei* Collignon appears to be the earliest available name. Collignon's material from the Lower Cenomanian of Madagascar consists of about 25 small pyritized specimens of 10–20 mm diameter. He referred some of them to *Desmoceras latidorsatum*, but for the slightly more compressed ones the new species *D. lemoinei* was proposed. All are more compressed than the Upper Albian subspecies, and they have weakly-developed constrictions. The holotype of *D. lemoinei* has the following approximate dimensions: diameter 11 mm, whorl height 6·1 mm, whorl breadth 5·6 mm; whorl height/breadth ratio 1·09. Similar, slightly compressed, specimens are found rarely in the Lower Cenomanian condensed facies of south and south-west England (Wright & Kennedy 1984).

The same, slightly compressed, subspecies occurs in the Lower Cenomanian of Japan, where it is said to be common, and was described as *D. kossmati* Matsumoto (1942, 1954). Specimens are larger, attaining 50–60 mm diameter, and the whorl height/breadth ratio again falls below that of the Upper Albian subspecies. The same name was used by Matsumoto (1959) for examples from the Lower Cenomanian of California. Similar specimens occur in the Lower Cenomanian of Texas and have been described as *D.* (*Pseudouhligella*) *elgini* Young (1958); these have even more compressed whorls, with height/breadth ratios in the range 1·15 to 1·55 at 15–30 mm diameter, but they overlap substantially with Lower Cenomanian collections from other areas and it is likely that *elgini* is also a synonym of *D. latidorsatum lemoinei.*

Superfamily **HOPLITACEAE** H. Douvillé, 1890

Family **PLACENTICERATIDAE** Hyatt, 1900

Genus ***PROPLACENTICERAS*** Spath, 1926

TYPE SPECIES. *Placenticeras fritschi* Grossouvre, 1894.

Proplacenticeras stantoni (Hyatt) var. ***bolli*** (Hyatt)

Fig. 7

1876 *Placenticeras intercalare* Meek: 471 (pars).
1903 *Placenticeras stantoni* var. *bolli* Hyatt: 214; pl. 40, figs 3–7; pl. 41, figs 1–7; pl. 42, figs 1, 2; pl. 43, figs 1, 2.
? 1930 *Placenticeras merenskyi* Haughton: 363; pl. 11, figs 1–3.
1942 *Proplacenticeras stantoni* var. *bolli* (Hyatt) Moreman: 219.
1965 *Proplacenticeras memoriaschloenbachi* (Laube & Bruder) var. *ambiloensis* Collignon: 14; pl. 381, fig. 1646.
1965 *Proplacenticeras stantoni* (Hyatt) var. *bolli* (Hyatt); Collignon: pl. 383, fig. 1651.

MATERIAL. One specimen, C.81058, from loc. 1007.

DESCRIPTION. The specimen is wholly an internal mould, and consists of one-third of a whorl of body chamber, starting at the final septum of the phragmocone at a whorl height of 67·5 mm, and ending at an irregularly broken aperture at a whorl height of about 80 mm. The latter corresponds to an overall diameter of about 175 mm, and the whorl breadth at that size is about 49 mm. Only part of the small umbilicus is preserved, because there is a break about halfway down the umbilical wall. The umbilical edge is rounded and merges into the whorl side. The greatest whorl breadth is near the umbilical edge, and from there the nearly flat whorl sides converge towards the venter, which is narrow and tabulate. The ventrolateral edges are well marked but rounded. The surface of this internal mould is smooth except for very faint traces of sinuous growth lines, one of which is accentuated almost to the strength of a constriction, especially on the outer half of the whorl and across the venter. The venter is smooth except for a very faint trace of a central ridge. The impressed dorsum shows that the venter of the next inner whorl was slightly concave between sharply-angled and slightly raised ventrolateral edges on which were a series of low undulating clavi that alternated from side to side.

The last septum has most of the saddles preserved, but the deeper (posterior) parts of the lobes are missing. The first lateral saddle is divided into three by two adventitious lobes, and it slopes backwards to the first lateral lobe which is the deepest part of the suture-line. The second lateral saddle and the two or three auxiliary saddles slope forwards again towards the umbilicus.

REMARKS. The Angolan specimen is only part of a large body chamber, but it is identified on the basis of its being an exact match with the final portion of a very fine complete specimen (BM(NH) C.53926) from the Britton Formation, Eagle Ford Group, near Britton, Texas. The latter specimen was obtained from W. S. Adkins and was labelled by him. Comparison of the two shows that the apparent umbilical seam of the Angolan specimen is in fact a curved break halfway down the umbilical wall, and the real umbilicus was somewhat smaller. Umbilical tubercles are not seen, probably because they faded just before the body chamber, as in the Texas specimen where they are well developed on the earlier whorls. The impression of the next inner whorl shows alternating clavi bounding a slightly concave venter, features that are typical of *Proplacenticeras*.

The correct name for this species depends on further taxonomic work to investigate the relationships between three names currently in use for specimens from the Britton Formation in Texas. These are *Proplacenticeras cumminsi* (Cragin 1893), *P. stantoni* var. *bolli* (Hyatt 1903) and *P. pseudoplacenta* var. *occidentale* (Hyatt 1903), as described by Moreman (1942: 219). The oldest name (*P. cumminsi*) depends on the interpretation of an unfigured holotype, while the two Hyatt names still await the designation of type specimens. In view of the large amount of variation found within Campanian species of *Placenticeras* by Wolleben (1967), it is possible that only one species of *Proplacenticeras* was present in the Lower Turonian Britton Formation in Texas. Until such a revision is done, the name attached to the Angolan specimen is that of the best figured of Hyatt's forms. Another similar specimen, though perhaps with a somewhat more complicated suture-line, has been described as *Proplacenticeras* cf. *pseudoplacenta* (Hyatt) by Matsumoto & Miller (1958: 355; pl. 45, fig. 2), and is part of a mid-Turonian (Woolgari Zone) assemblage of ammonites from Texas.

A single specimen from Namibia that was made the holotype of *Placenticeras merenskyi* by Haughton (1930: 363; pl. 11, figs 1–3) is very close in all visible features to the inner whorls of the Texas specimens, and the specific name is probably a synonym. Its Upper Cenomanian age is deduced from an associated fauna of *Exogyra*. Other examples of *Proplacenticeras* occur in Madagascar, and at least some of those figured by Collignon (1965: pl. 381, fig. 1646; pl. 383, fig. 1651) are probably the same as the Texas species. Different species of *Proplacenticeras* are abundant in the Coniacian of south-east Africa, but Turonian rocks are not known in that area (Kennedy & Klinger 1975: 278). Species of *Proplacenticeras* in the Upper Cenomanian of Europe are *P. memoriaschloenbachi* (Laube & Bruder) and *P. orbignyanum* (Geinitz), both being more compressed than *P. stantoni* var. *bolli*.

OCCURRENCE. Lower Turonian of Angola, Namibia, Madagascar and Texas.

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894

Family **FORBESICERATIDAE** Wright, 1952

Genus ***FORBESICERAS*** Kossmat, 1897

TYPE SPECIES. *Ammonites largilliertianus* d'Orbigny, 1841.

Forbesiceras obtectum (Sharpe)
Fig. 14

1853 *Ammonites obtectus* Sharpe: 20; pl. 7, fig. 4.
1971 *Forbesiceras obtectum* (Sharpe); Kennedy: 47; pl. 9, fig. 3; pl. 16, fig. 3; pl. 46, fig. 3 (see for synonymy).
1973 *Forbesiceras obtectum* (Sharpe); Cooper: 48; fig 5, 6A, 6B.
1984 *Forbesiceras obtectum* (Sharpe); Wright & Kennedy: 94; pl. 12, fig. 4; pl. 14, figs 1, 2; pl. 15, fig. 4.

MATERIAL. Eight specimens, C.81077 from loc. 275, C.81078–83 from loc. 419, and C.81084 from loc. 953.

REMARKS. This species has been described by Kennedy (1971), who gave a full synonymy, and by Cooper (1973), who had a considerable number of large specimens from localities near Novo Redondo. The present collection consists of eight large, worn internal moulds, all wholly septate, and with no portion of the original shell or ornament preserved. The most complete specimen has much of one whorl preserved up to a maximum size of 205 mm diameter, while all the others are large fragments of a quarter of a whorl or less, the largest having a whorl height of 150 mm and breadth of 54 mm, which corresponds to a diameter of about 225 mm. The largest specimen recorded by Cooper was 305 mm in diameter.

OCCURRENCE. Middle Cenomanian of England, Angola and many other areas of Asia and Africa. Well dated occurrences are Middle Cenomanian, but the species may also occur in the Lower Cenomanian (see Wright & Kennedy 1984: 95).

Family **ACANTHOCERATIDAE** Grossouvre, 1894

Subfamily **MANTELLICERATINAE** Hyatt, 1903

Genus ***SHARPEICERAS*** Hyatt, 1903

TYPE SPECIES. *Ammonites laticlavius* Sharpe, 1855.

DISCUSSION. This genus and its type species have been discussed by Matsumoto, Muramoto & Takahashi (1969: 258) and Kennedy (1971: 64). Characteristic features are the high, flat-sided whorls, long ribs, and umbilical, mid-lateral and lower and upper ventrolateral tubercles. A second lateral tubercle may appear above the mid-lateral position. The ventrolateral tubercles enlarge into horns in the adults of some species, and the ribs become widely spaced. Such massive-whorled, horned adults are usually between 200 mm and 400 mm in diameter.

Sharpeiceras appears to have been derived at the base of the Lower Cenomanian from early *Mantelliceras* stock, by the development of a mid-lateral tubercle at small diameters which was retained throughout growth. *Sharpeiceras* is an uncommon genus in most areas, but it is of widespread distribution and is restricted to the lower and middle zones of the Lower Cenomanian, and so is an accurate age indicator (Kennedy & Hancock 1977: 132, 1978: V.14).

Sharpeiceras florencae Spath
Figs 15–19

1904 *Acanthoceras laticlavium* (Sharpe); Douvillé: 239; pl. 31, fig. 3.
1925 *Sharpeiceras florencae* Spath: 198, pl. 37.
? 1931 *Acanthoceras* (*Mantelliceras*) *falloti* Collignon: 41; pl. 4, figs 9–12.
1933 *Sharpeiceras florencae* Spath; Collignon: 67; pl. 6, fig. 5.
1942 *Sharpeiceras goliath* Haas: 7; figs 5–7.
? 1956 *Sharpeiceras occidentale* Benavides-Cáceres: 465; pl. 54, figs 5, 6.
1959 *Sharpeiceras florencae* Spath; Matsumoto: 69, 70; fig. 28.
1962 *Tlahualitoceras tlahualitoense* Kellum & Mintz: 276; pl. 6, fig. 1; pl. 7, figs 1, 2; pl. 8, fig. 1.
1964 *Sharpeiceras schlueteri* Hyatt; Collignon: 102; pl. 353, fig. 1564.
? 1964 *Sharpeiceras vohipalense* Collignon: 104; pl. 354, fig. 1565.
1971 *Sharpeiceras florencae* Spath; Kennedy: 67; pl. 25, fig. 2.
1982 *Sharpeiceras occidentale* Benavides-Cáceres; Renz: 68; pl. 21, fig. 1.

MATERIAL. 13 specimens: C.80975 from loc. 67, C.80977 from loc. 72, C.80979–80 from loc. 76, C.80990–1 and C.81005 from loc. 88, C.81000 from loc. 99, C.81003–4 from loc. 100, C.81006 from loc. 102, C.81016 from loc. 188, and C.81052 from loc. 526.

MEASUREMENTS.	D	Wh	Wb	U	Wh/Wb
C.81006	192·5	77·7 (0·40)	58·3 (0·30)	56 (0·29)	1·33
C.81005	—	79	63·5	—	1·24
C.80979	—	89	74	—	1·20
C.81003	—	56	44	—	1·27

DESCRIPTION. The most complete specimen (C.81006, Fig. 17) is 208 mm in diameter at the aperture. Owing to poor preservation septa cannot be seen, though it appears to have between a quarter and half a whorl of body chamber. The ribs and tubercles are of moderate strength up to about 135 mm diameter, then they become much stronger and more widely spaced. From the same size the lower ventrolateral tubercle becomes much enlarged into a horn, to such an extent

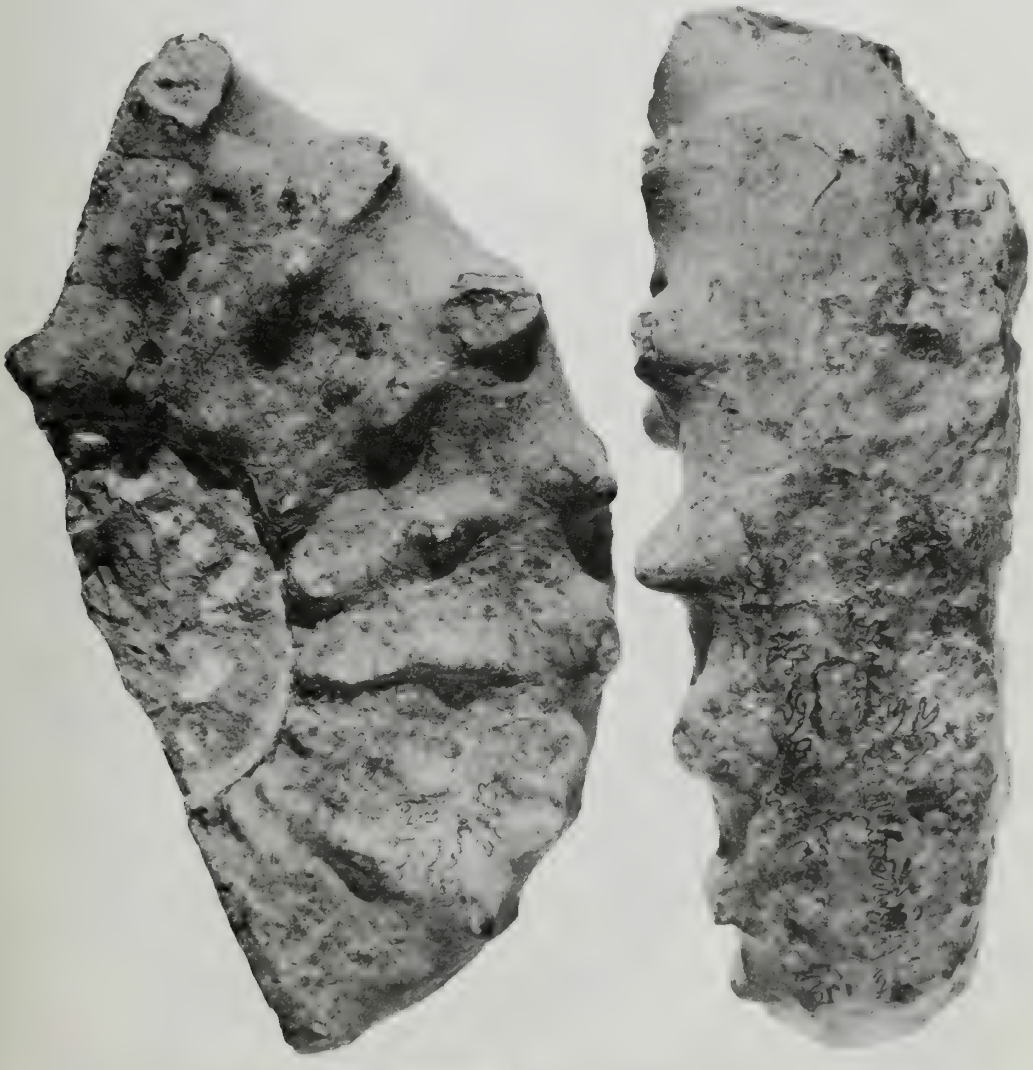


Fig. 15 *Sharpeiceras florencae* Spath from Lower Cenomanian at loc. 88. C.81005, ×0·57.

that it merges with the upper ventrolateral tubercle. The mid-lateral tubercle also becomes considerably enlarged. It has 25 or 26 ribs on the outer whorl at 208 mm diameter. All the other specimens are fragments of less than half a whorl (Figs 15, 16, 18, 19), though in general they are better preserved and all have septa. One of the two largest specimens (C.81005, Fig. 15) has about one-sixth of a whorl of body chamber, while the other specimen is wholly septate, indicating that the phragmocone reached at least 280 mm diameter. Up to sizes of about 135 mm diameter both long and short ribs occur, the short ribs starting at about the level of the lateral tubercle (C.81016, Fig. 18), and consequently there are more ventrolateral than umbilical tubercles, though never twice as many. At sizes larger than 135 mm diameter nearly all the ribs become long. The umbilical tubercles are always the smallest and even tend to disappear at the largest diameters. There is considerable variation in the position of the lateral tubercles, from somewhat below to slightly above the mid-lateral position.

DISCUSSION. The large, much worn, holotype of *Sharpeiceras goliath* Haas (1942: 7, fig. 7), the only example of *Sharpeiceras* recorded previously from Angola, was from a locality about 45 km ESE of Luanda. The species is almost certainly a synonym of *S. florencae*, for it agrees in whorl proportions, rib style and density, and develops the same large horns. The only difference referred to by Haas was the development of a low blunt keel, visible on the shell of *S. goliath* but not on the internal mould. However, this is a variable feature in the new collection described here and is due to the variable preservation of the siphuncle. Haas' specimen is probably the only known example of an adult body chamber of *S. florencae*, and it shows that the whorl section becomes trigonal on adults at sizes of more than 300 mm diameter. *S. mexicanum* (Böse), described below, is always more compressed and has much smaller tubercles. *S. laticlavium* (Sharpe), the type of the genus, differs in having more ribs and does not develop the coarsening of the ornament on the body chamber. Two other similar species are *S. schlueteri* Hyatt, which is more evolute and does not develop widely spaced ribs or large horns, and *S. laticlavium* var. *indica* Kossmat (1895: 199; pl. 24, figs 5, 6), which is more compressed, has mainly single ribs and lacks the coarse ornament.

S. falloti (Collignon) is based on small specimens that are probably juveniles of *S. florencae*. *S. occidentale* Benavides-Cáceres is based on a single fragment of *S. florencae* from Peru, and a more complete specimen from Venezuela was figured by Renz (1982: 68; pl. 21, fig. 1). As suggested by Kennedy (1971: 64) *Tlahualitoceras tlahualitoense* Kellum & Mintz shows no features whereby it may be distinguished from *S. florencae*. Two Madagascan specimens figured by Collignon (1964: figs 1564–5) also belong here: one of them (fig. 1565) is 162 mm in diameter and has developed especially widely spaced ribs and large horns on the final quarter of a whorl. An even more heavily tuberculate species is *S. kongo* Matsumoto, Muramoto & Takahashi (1969: 261; pl. 29, fig. 1; pl. 30, fig. 1) in Japan. At sizes between 200 mm and 300 mm diameter the inner ventrolateral tubercles are enlarged into very large, ventrally-pointing, clavate horns, while the outer ventrolateral tubercles remain separate and smaller. In these respects *S. kongo* differs substantially from *S. florencae*.

OCCURRENCE. *Sharpeiceras florencae* is currently known from Mozambique, Madagascar, Zululand, Angola, Mexico, Peru, North America and southern England.

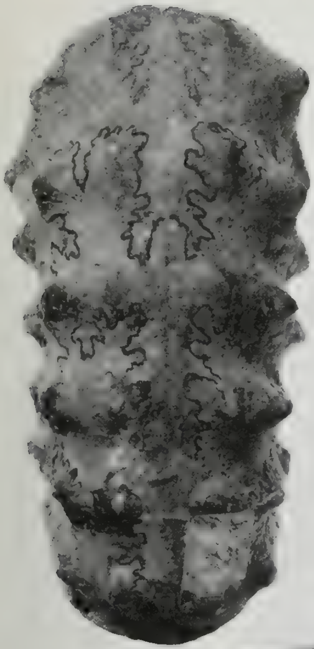
Sharpeiceras mexicanum (Böse)
Figs 20, 23

1928 *Mantelliceras laticlavium* (Sharpe) var. *mexicanum* Böse: 253; pl. 10, fig. 6; pl. 11, fig. 1.

MATERIAL. 4 specimens: C.80999 from loc. 90, C.81001–2 from loc. 99, C.81007 from loc. 102.

MEASUREMENTS.	D	Wh	Wb	U	Wh/Wb
C.81007	127	55·4 (0·44)	38·2 (0·30)	34 (0·27)	1·45
C.81001	—	73	39	—	1·87

Figs 16, 17 *Sharpeiceras florencae* Spath from Lower Cenomanian. Fig. 16, loc. 100, C.81003, ×0·8; Fig. 17, loc. 102, C.81006, ×0·6.



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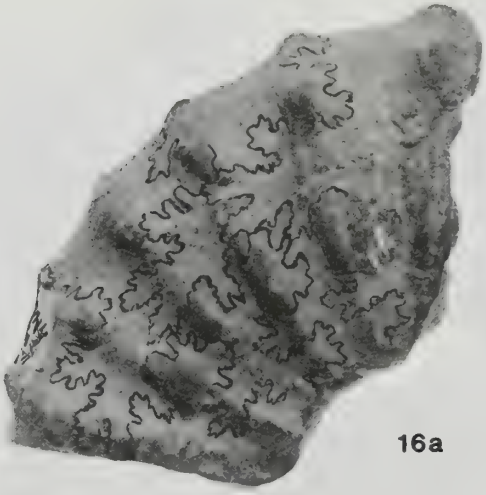

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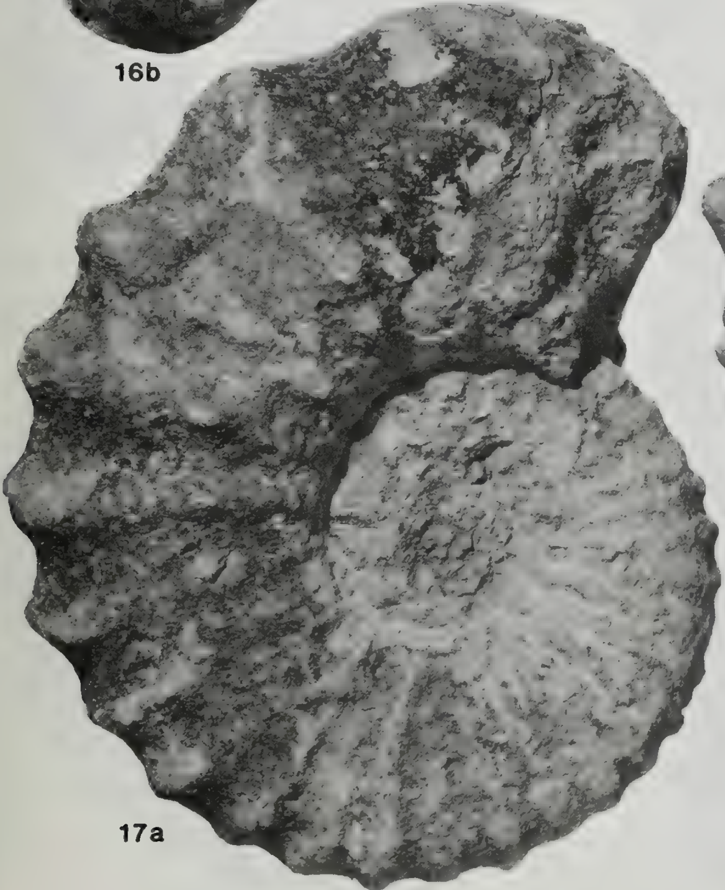

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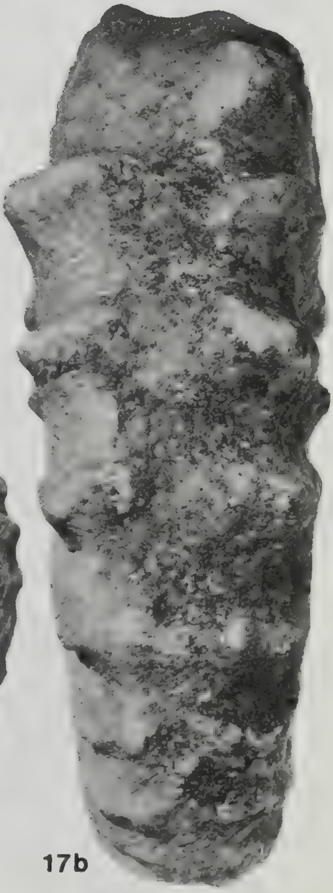

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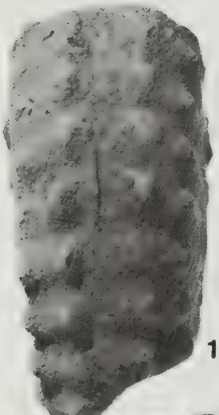
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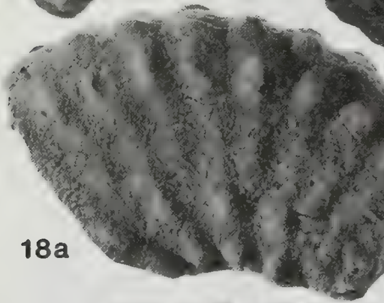
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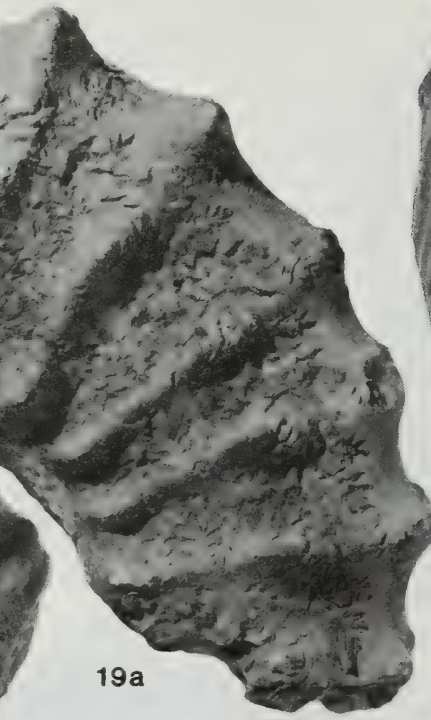
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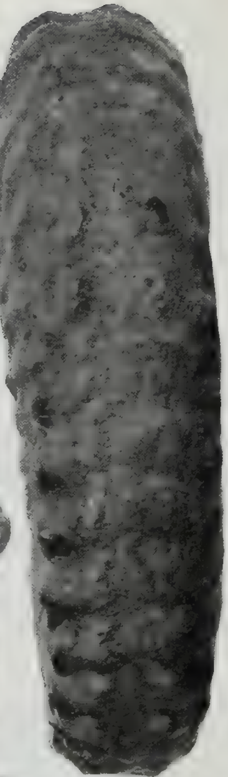
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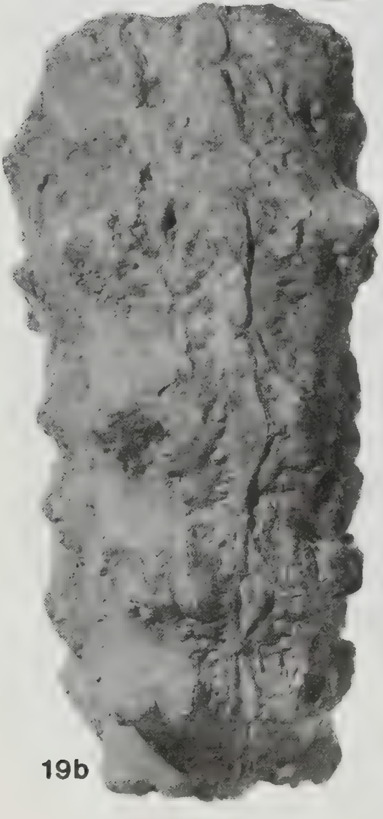
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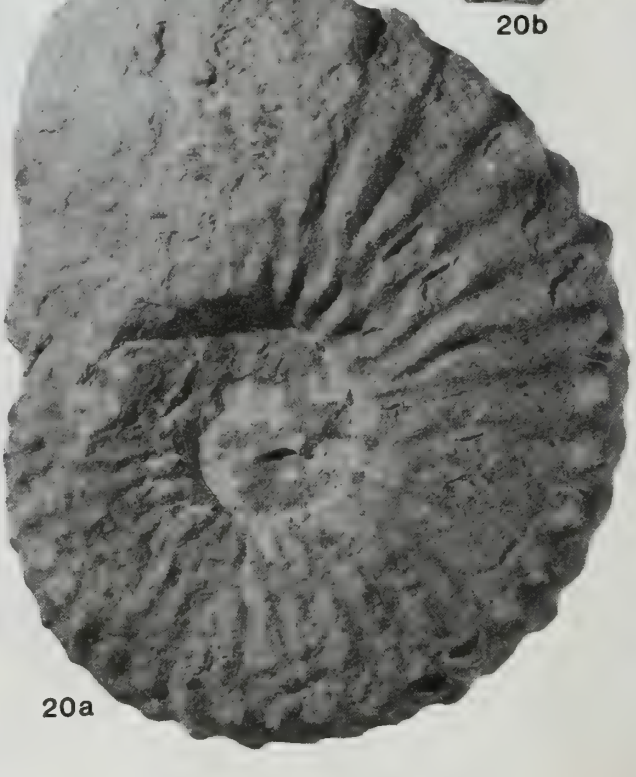
20a

Description. The collection consists of one complete specimen (C.81007, Fig. 20) and three septate fragments. The complete specimen is septate up to 94 mm diameter, at which size the whorl height is 40 mm, then nearly half a whorl of body chamber ends at 137 mm diameter at the aperture. It is probably immature. The three septate fragments have whorl heights up to about 85 mm, showing that the species attained much larger sizes when fully grown. The whorls are compressed and quadrate with flat sides and flat venter. The ratio of whorl height to whorl breadth varies between 1·45 and 1·90. The complete specimen has about 35 ribs per whorl at 135 mm diameter, and the fragments have ribbing of similar density. Most ribs are prorsiradiate up to the lateral tubercle where they bend slightly backwards and become radial or rursiradiate on the outer half of the side of the whorl. Some ribs are long and single, others arise in pairs from an umbilical tubercle, and there are occasional intercalated ribs starting from a lateral tubercle. The ratio of long to short ribs is such that 10 umbilical tubercles are represented by 14 lateral tubercles in the complete specimen. The umbilical and lateral tubercles are small, the latter being situated about one-third of the distance between the umbilicus and the venter. The inner ventrolateral tubercle is small and clavate; the outer ventrolateral tubercle is of medium size, and does not attain the large sizes seen in other species.

Discussion. *S. mexicanum* is more compressed than *S. florencae*, and the ribs remain dense and the tubercles are small even on the largest fragments. At similar large sizes *S. florencae* has widely-spaced ribs and much larger lateral and ventrolateral horns. *S. mexicanum* is more compressed than *S. laticlavium* (Sharpe) and has more bifurcating or intercalated ribs. *S. laticlavium* var. *indica* (Kossmat) is similarly compressed, but has fewer and larger ribs. *S. schlueteri* Hyatt (Schlüter 1871: 18; pl. 7, figs 4–8) is more evolute. An apparently similar species is *Graysonites byzenica* (Pervinquière 1907: 302; pl. 14, fig. 4), but it is more involute and every rib bifurcates from a small umbilical tubercle; it is referred to *Graysonites* because mid-lateral tubercles are absent. No examples of the adult body chamber of *S. mexicanum* are known, so it is not possible to determine whether it becomes less densely ribbed and more strongly tuberculate when fully grown, like most species of *Sharpeiceras*.

Genus ***CALYCOCERAS*** Hyatt, 1900

Type species. *Ammonites navicularis* Mantell, 1822.

Discussion. This genus and its subdivision into subgeneric groups has been fully discussed by Kennedy (1971: 70) and Cooper (1978*a*: 83–85).

Calycoceras (Calycoceras) naviculare (Mantell)
Fig. 21

1822 *Ammonites navicularis* Mantell: 198; pl. 22, fig. 5.
1971 *Calycoceras naviculare* (Mantell); Kennedy: 71; pls 33–36; pl. 37, figs 1–3; pl. 47, figs 1, 3, 5.
1971 *Calycoceras naviculare* (Mantell); Cobban: 13; pl. 1, figs 1–3; pls 10–17.
1978*a* *Calycoceras naviculare* (Mantell); Cooper: 85; figs 4L, 4M, 12A, 15A, 17, 18A, 18B.
1981 *Calycoceras* (*Calycoceras*) *naviculare* (Mantell); Wright & Kennedy: 34–36; pl. 4; pl. 5, figs 1–3; text-figs 13, 14c–e.

Material. A single specimen, C.81066 from loc. 1007.

Description. The specimen consists of a wholly septate fragment about one-third of a whorl long, from a whorl about 100 mm diameter. It is preserved mainly as an internal mould. Though parts of both sides of the whorl are missing, most of the venter is intact, and it is almost uncrushed. At the smaller end, the whorl height is 39·5 mm and the whorl breadth 58 mm. The

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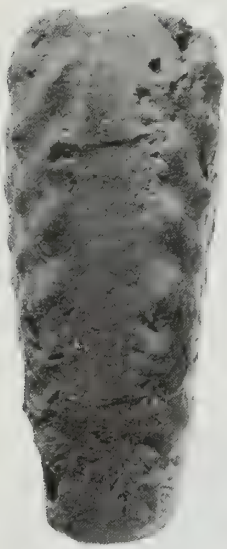
Figs 18, 19 *Sharpeiceras florencae* Spath from Lower Cenomanian. Fig. 18, loc. 188, C.81016, ×1; Fig. 19, loc. 76, C.80979, ×0·58.

Fig. 20 *Sharpeiceras mexicanum* (Böse) from Lower Cenomanian at loc. 102. C.81007, ×0·8.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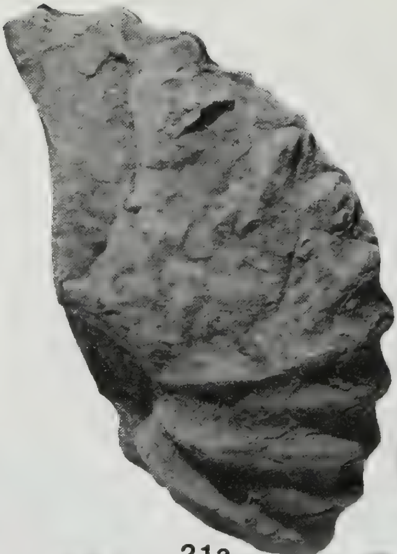
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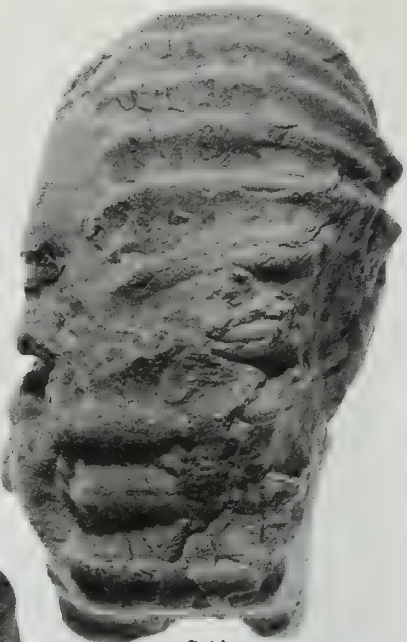
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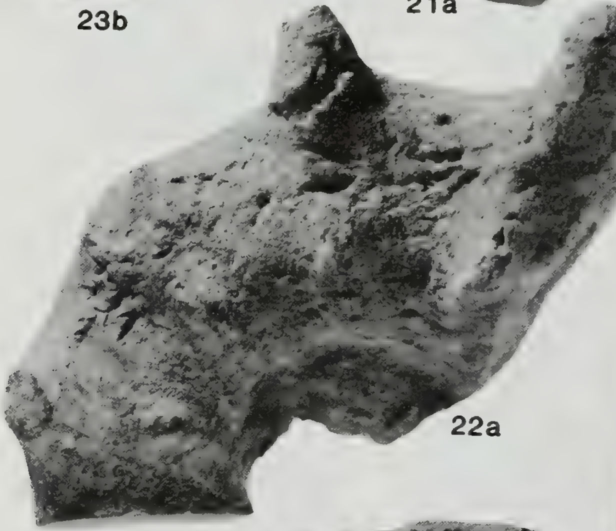
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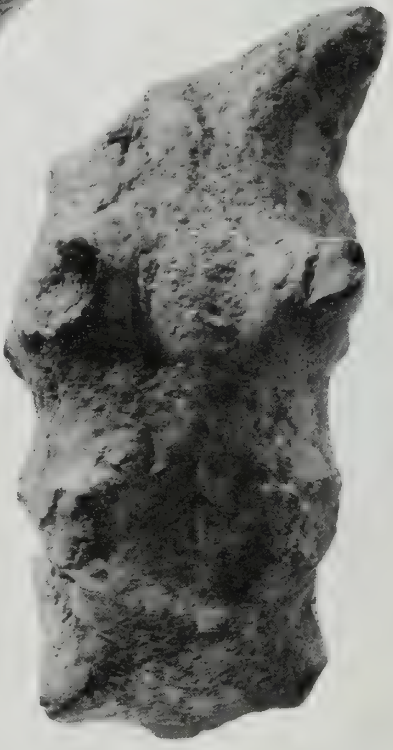
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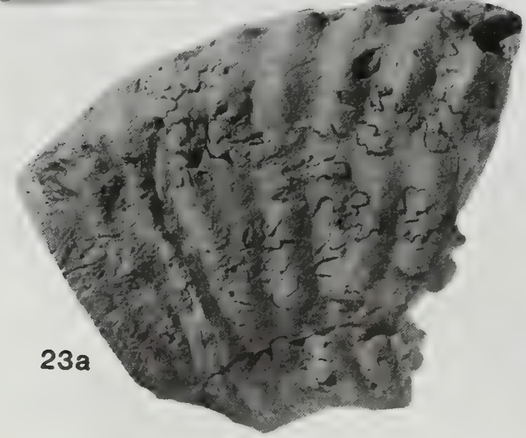

23a

whorl height/breadth ratio is 0·68, which is typical of the species at about this size. The fragment has the remains of six robust primary ribs and six umbilical bullae, and with an equal number of shorter intercalated ribs there are 12 ribs of equal size on the venter. The ribs are slightly angled at the ventrolateral edge. The whorl section is widest at the umbilical bullae, the umbilical walls are evenly convex, and the whorl sides curve smoothly to join the almost flat venter which is about one-third of the total width.

DISCUSSION. Full descriptions of material much more abundant than that described here can be found in Cobban (1971), Kennedy (1971), Cooper (1978*a*) and especially in Wright & Kennedy (1981), who all give extended synonymies. The species has been found commonly in Angola and several specimens have been figured before by Douvillé (1931, as *Acanthoceras borgesi*) and Cooper (1978*a*).

OCCURRENCE. *Calycoceras naviculare* occurs in the Upper Cenomanian and is widespread in many parts of the world (Kennedy & Hancock 1978: V.16, Wright & Kennedy 1981: 36).

Subfamily **EUOMPHALOCERATINAE** Cooper, 1978

Genus ***EUOMPHALOCERAS*** Spath, 1923

TYPE SPECIES. *Ammonites euomphalus* Sharpe, 1855.

DISCUSSION. Cooper (1978*a*) proposed the new subfamily Euomphaloceratinae to include the following evolute, commonly constricted, multituberculate derivatives of *Acanthoceras: Euomphaloceras* (*Euomphaloceras*), *E.* (*Kanabiceras*), *Kamerunoceras* (including its synonym *Schindewolfites*), *Yubariceras, Romaniceras, Obiraceras* and *Shuparoceras*, which split from the Acanthoceratinae high in the Middle Cenomanian.

The large amount of variation in both *E.* (*E.*) *euomphalus* (Wright 1963: 609, Kennedy 1971: 91) and *E.* (*Kanabiceras*) *septemseriatum* (Cragin) (Matsumoto 1959, Powell 1963, Cobban & Scott 1972, Cooper 1978*a*) makes some individuals difficult to separate, especially as passage forms are known. In *E.* (*K.*) *septemseriatum*, however, the siphonal tubercles commonly form a serrated keel, whilst it does not develop the square whorls and large ventrolateral tubercles that are shown by *E. euomphalus* in maturity (Wright 1963: pl. 88).

Kamerunoceras differs from *E.* (*Kanabiceras*) in that the number of siphonal tubercles corresponds to the number of upper ventrolateral tubercles (at least when mature), whereas in *E.* (*Kanabiceras*) the siphonal tubercles are more numerous.

Subgenus ***EUOMPHALOCERAS*** Spath, 1923

Euomphaloceras* (*Euomphaloceras*) *cunningtoni (Sharpe) var. ***meridionale*** (Stoliczka)

Figs 22, 24

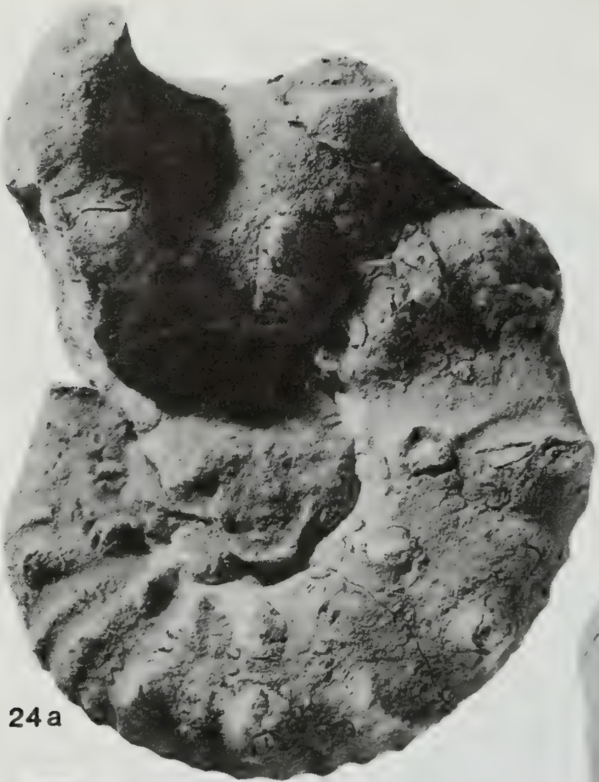
1864 *Ammonites meridionalis* Stoliczka: 76; pl. 41, figs 1a–c.
1907 *Acanthoceras meridionale* (Stoliczka) Pervinquière: 278; pl. 15, figs 2–4.
1963 *Euomphaloceras cunningtoni meridionale* (Stoliczka) Wright: 608; pl. 89, fig. 1.
1969 *Euomphaloceras meridionale* (Stoliczka); Matsumoto, Muramoto & Takhashi: 272; pl. 33, figs 1–2; pl. 34, fig. 1.
1971 *Euomphaloceras cunningtoni meridionale* (Stoliczka); Kennedy: 93
1973 *Euomphaloceras cunningtoni meridionale* (Stoliczka); Cooper: 61; figs 10A–B, 11, 12A–B, 13A.

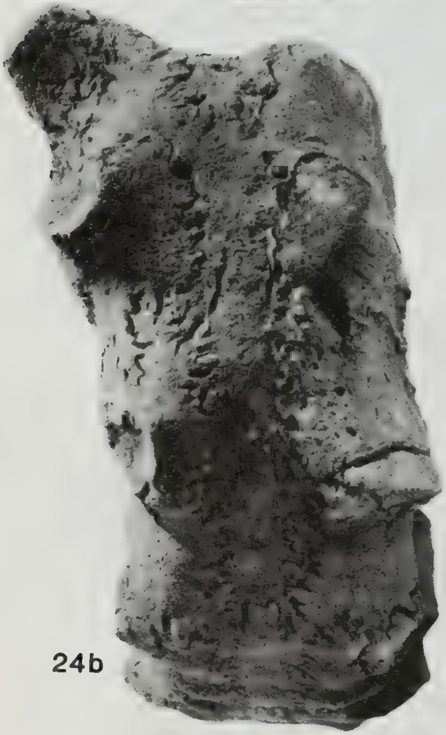
MATERIAL. Five specimens: C.81017 and C.81039 from loc. 263, C.81018 from loc. 275, C.81042 from loc. 430, and 81057 from loc. 953.

Fig. 21 *Calycoceras* (*C.*) *naviculare* (Mantell) from Upper Cenomanian at loc. 1007. C.81066, ×0·77.

Fig. 22 *Euomphaloceras* (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka) from Middle Cenomanian at loc. 430. C.81042, ×0·68.

Fig. 23 *Sharpeiceras mexicanum* (Böse) from Lower Cenomanian at loc. 99. C.81001, ×0·78.


24 a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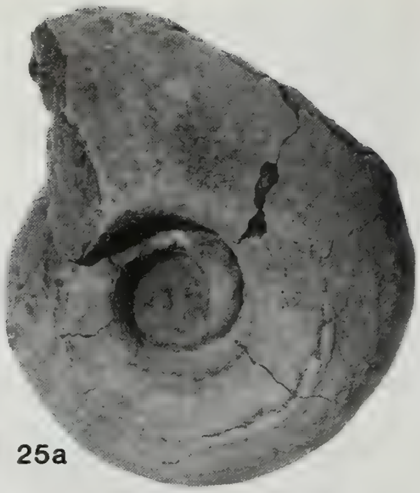
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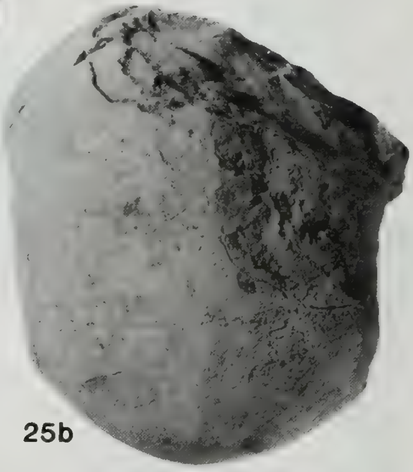
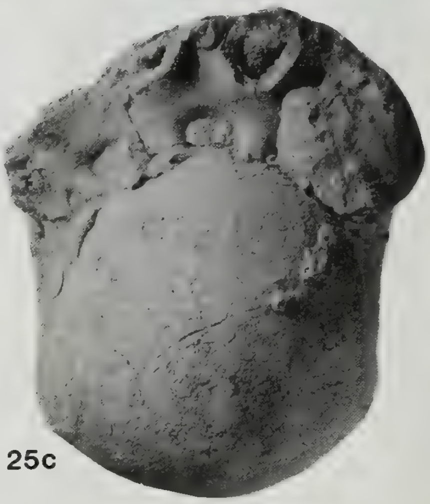

25b


25c

Description. The collection consists of a specimen (C.81057, Fig. 24) which is wholly septate at its aperture at 126 mm diameter, and four poorly-preserved fragments, of which C.81017 has its final septum at 165 mm diameter followed by a short length of worn body chamber. The largest fragment (C.81042) is a short piece of body chamber that has a whorl height of about 87 mm. The whorl cross section is quadrate and depressed. The ribbing is much reduced, though both primary and intercalated ribs can be seen up to about 80 mm diameter. At larger sizes the tuberculation is entirely dominant, and consists of umbilical tubercles, large ventrolateral horns, small upper ventrolateral tubercles and small siphonal tubercles. There are equal numbers of upper ventrolateral and siphonal tubercles, which are between two and three times as frequent as either the umbilical tubercles or the ventrolateral horns. The tubercles on the venter tend to disappear after about 100 mm diameter and the ventrolateral horns become very large. There are 12 ventrolateral horns on the outer whorl of the figured C.81057 at 125 mm diameter.

Discussion. The species and its synonymy have been described by Kennedy (1971: 92), and several Novo Redondo specimens of the variety *meridionale* have been figured before by Cooper (1973). The present collection consists mainly of larger specimens, though most are not well preserved. The siphonal and upper ventrolateral tubercles occur in equal numbers, and it is this feature that distinguishes *meridionale* from the nominate variety of the species in which there are fewer upper ventrolateral tubercles.

Occurrence. In England *E. cunningtoni* occurs in the lower part of the Middle Cenomanian (Kennedy 1971: 94). It also occurs in France, north Africa, Madagascar, India, Japan, northern Australia and Texas.

Subgenus ***KANABICERAS*** Reeside & Weymouth, 1931

Type species. *Acanthoceras kanabense* Stanton, 1894 (= *Scaphites septemseriatum* Cragin, 1893).

Euomphaloceras (Kanabiceras) septemseriatum (Cragin)
Figs 26–29

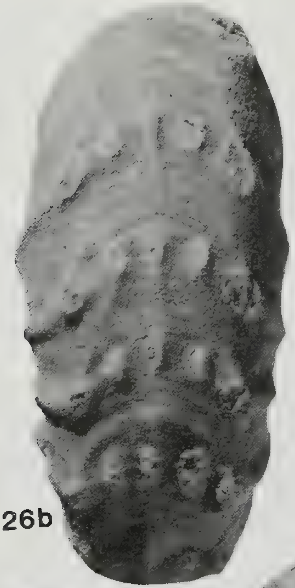
1893 *Scaphites septemseriatum* Cragin: 240.
1894 *Acanthoceras kanabense* Stanton: 181; pl. 36, figs 6–8.
1927 *Acanthoceras kanabense* Stanton; Moreman: 95; pl. 13, fig. 5.
1931 *Kanabiceras kanabense* (Stanton) Reeside & Weymouth: 11.
1931 *Prionotropis echinatus* Douvillé: 34; pls 3, 4.
1942 *Neocardioceras septemseriatum* (Cragin) Moreman: 213; pl. 33, figs 11, 12.
1958 *Lyelliceras stanislausense* Anderson: 247; pl. 8, fig. 5.
1959 *Kanabiceras septemseriatum* (Cragin); Matsumoto: 99; pl. 24, fig. 1.
1963 *Kanabiceras septemseriatum* (Cragin); Powell: 316; pl. 31, figs 9, 10.
1969 *Kanabiceras septemseriatum* (Cragin); Matsumoto, Muramoto & Takahashi: 279; pl. 37, figs 1–3.
1972 *Kanabiceras septemseriatum* (Cragin); Cobban & Scott: 72; pl. 12, figs 5–27.
1978*a* *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin) Cooper: 106; figs 4N–O, 10A–E, 12E–H, 18G–H, 19G–L, 26A–B, 28.
1981 *Euomphaloceras septemseriatum* (Cragin); Wright & Kennedy: 55; pl. 12, figs 1–8; pl. 13, figs 1–6; pl. 14, figs 5–9.

Material. Six specimens: C.81059–64 from loc. 1007.

Description. The collection consists of the internal moulds of six body chamber fragments. In four of them the final septum is followed by one-quarter to one-third of a whorl of body chamber

Fig. 24 *Euomphaloceras* (*E.*) *cunningtoni* (Sharpe) var. *meridionale* (Stoliczka) from Middle Cenomanian at loc. 953. C.81057, ×0·8.

Fig. 25 *Vascoceras* (*Paravascoceras*) *harttii* (Hyatt) from Lower Turonian at loc. 1007. C.81075, ×0·8.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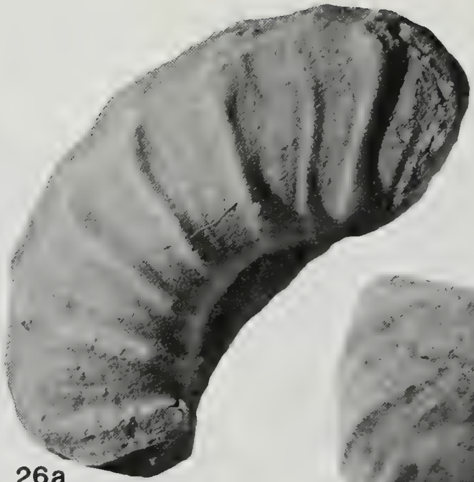
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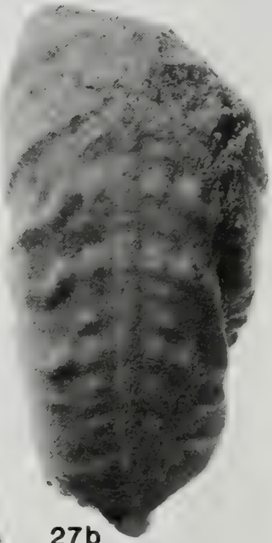
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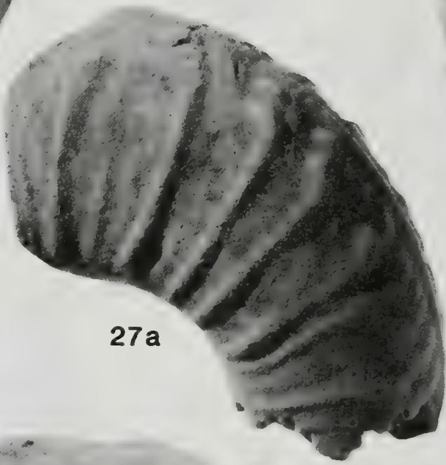
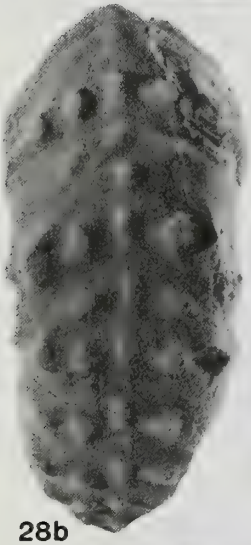

27a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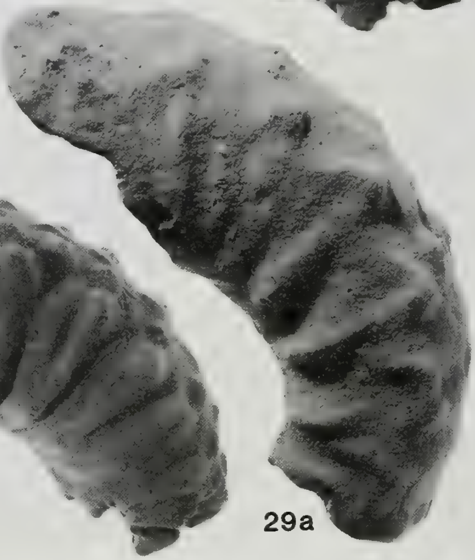
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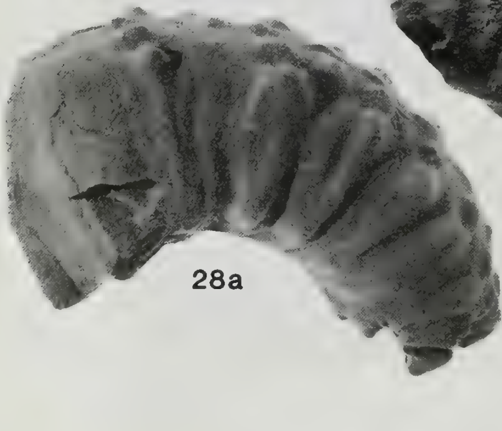
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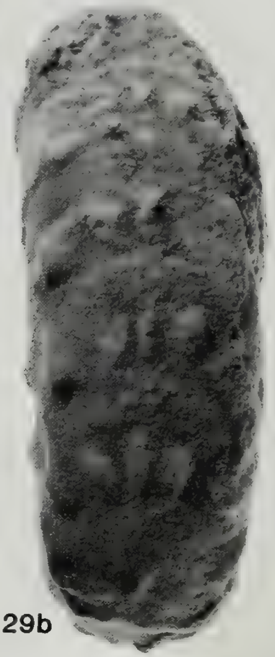
29b

up to the broken aperture, while the other two are entirely non-septate. The largest has a final diameter estimated as about 105 mm. If body chambers were half to two-thirds of a whorl in length when complete, then the diameter at the adult mouth borders would be in the range100–125 mm. The whorl section is subtrapezoidal, depressed, with maximum width at the position of the umbilical tubercles.

The ornament consists of moderately strong ribs that curve forwards at the ventrolateral edge and become much diminished in strength and subordinate to the tubercles on the venter. Small umbilical tubercles are situated at or slightly above the umbilical edge. The lower ventrolateral tubercles are large and sometimes obliquely clavate, and are connected by weak ribs to the smaller upper ventrolateral tubercles situated on the venter. In some specimens the number of upper ventrolateral is equal to the number of lower ventrolateral tubercles, while in others the upper ventrolateral tubercles are more numerous (cf. Figs 26b and 27b). The ventral keel varies between weak and moderately strong, and is ornamented by weak to moderate siphonal tubercles which are usually equal in number to the upper ventrolateral tubercles.

An external mould of the inner whorls of C.81061 shows that there are about 35 strong, slightly prorsiradiate ribs at about 40 mm diameter, which become much more distant on the body chamber.

Discussion. This collection of adult body chambers complements the collection of smaller Salinas specimens that were described by Cooper (1978*a*: 106), and which were mainly phragmocones. Many authors (e.g. Matsumoto 1959: 101, Powell 1963: 316, Cobban & Scott 1972: 72, Cooper 1978*a*: 107) have remarked on the large amount of variation in this species, and here it can be seen that all six body chambers are different in rib density, in strength and number of tubercles, and in the strength of the siphonal keel. Wright & Kennedy (1981: 55) said that *Kanabiceras septemseriatum* was not worthy of more than specific distinction from *Euomphaloceras euomphalus*. However, the differences between the large horned examples of *Euomphaloceras* (e.g. Fig. 22) and the multituberculate body chambers of *Kanabiceras* (Figs 26–29) seem to be sufficiently large to justify the subgeneric distinction adopted here.

Occurrence. This species is characteristic of the top part of the Upper Cenomanian, and has a widespread distribution in North America, Africa, western Europe and Japan.

Subfamily **MAMMITINAE** Hyatt, 1900

Genus ***PSEUDASPIDOCERAS*** Hyatt, 1903

Type species. *Ammonites footeanus* Stoliczka, 1864.

Discussion. Both *Mammites* and *Pseudaspidoceras* contain species that display considerable variation in ribs, tubercles and whorl proportions, and several authors have had difficulty in drawing a clear distinction between the two genera. In general *Pseudaspidoceras* differs from *Mammites* in being more evolute, having strongly inflated, sometimes depressed whorls, and less regular ornament. Most species of *Pseudaspidoceras* have considerably more upper ventrolateral than lower ventrolateral tubercles at least on the phragmocone, and have a suture-line with narrow first and second lateral saddles and a very wide first lateral lobe. These two features are generally distinctive, though a few species of *Mammites* have a similar tubercle arrangement (e.g. *M. mutabilis* Reyment, 1955: 51; pl. 10, fig. 1). A comprehensive diagnosis for *Pseudaspidoceras* was given by Freund & Raab (1969: 13), and although there is an area where the two genera overlap, it is just possible to keep *Mammites* and *Pseudaspidoceras* as distinct genera. *Pseudaspidoceras* is confined to the Lower Turonian, and the small Angolan collection described here shows that the beds in which it was found are of that age.

Figs 26–29 *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin) from Upper Cenomanian at loc. 1007. All ×1. Fig. 26, C.81060; Fig. 27, C.81064; Fig. 28, C.81061; Fig. 29, C.81059.

Pseudaspidoceras footeanum (Stoliczka)
Figs 30–33

1864 *Ammonites footeanus* Stoliczka: 101; pl. 52, figs 1, 2.
1887 *Ammonites pedroanus* White: 212; pl. 22, figs 1, 2.
1918 *Pseudaspidoceras* aff. *pedroanum* (White) Böse: 209; pl. 13, fig. 1; pl. 15, fig. 1.
1936 *Pseudaspidoceras pedroanum* (White); Maury: 231; pl. 21, figs 1, 2.
1972 *Pseudaspidoceras pedroanum* (White); Reyment & Tait: pl. 3, fig. 12.
1978 *Pseudaspidoceras* aff. *pedroanum* (White); Chancellor, Reyment & Tait: 91; figs 8–10.
1981 *Pseudoaspidoceras* cf. *footeanum* (Stoliczka); Wright & Kennedy: 82; pl. 21, fig. 3.

MATERIAL. Seven specimens, C.81068–74, from loc. 1007.

MEASUREMENTS.	D	Wh	Wb	U	Wh/Wb
C.81069	—	48	52	—	0·92
C.81070	—	47	54·5	—	0·86
C.81072	—	50·8	51·8	—	0·98
C.81073	85·5	36·2 (0·42)	38 (0·44)	25·6 (0·30)	0·95
C.81074	—	36·5	42·8	—	0·85

DESCRIPTION. The seven specimens in the collection consist of four septate fragments and three body-chamber fragments. All are less than a quarter of a whorl in length, except for one badly eroded septate specimen of nearly half a whorl, and C.81073 (Fig. 30) which consists of three-quarters of a septate whorl 85 mm in diameter at the larger end. The whorls are quadrate and slightly depressed, and the greatest whorl breadth is over the umbilical tubercles. Ribs are poorly developed and subordinate to tubercles at all the sizes seen. Large umbilical tubercles are connected by low rounded ribs to large lower ventrolateral tubercles. The umbilical and lower ventrolateral tubercles are usually equal in number, though at sizes below 70 mm diameter there are occasional extra lower ventrolateral tubercles. The upper ventrolateral tubercles are smaller and between two and three times as frequent as the lower ventrolateral tubercles. On large body chambers the lower ventrolateral tubercles increase in size to become large horns which may absorb the corresponding upper ventrolateral tubercles. The suture-lines have a very wide first lateral lobe divided into two halves by a median saddle, and relatively long and narrow first and second lateral saddles.

DISCUSSION. This small collection of fragments differs only slightly from the holotype and only known specimen of *Mammites mocamadensis* Howarth (1968: 222; pl. 3). The latter has larger horns and whorls that are generally more massive. It was the only *Mammites* or *Pseudaspidoceras* previously recorded from Angola, and it was difficult to decide to which of the two genera it should be referred. However, like the present collection it does have the very wide first lateral lobe that is held to be characteristic of *Pseudaspidoceras*, and assignment to that genus is more appropriate.

The most complete specimen in the collection now described (C.81073, Fig. 30) and one of the larger fragments (C.81072, Fig. 32) both bear a close resemblance to the specimen figured by Stoliczka (1864: pl. 52, figs 1, 1*a*). The fragments of body chambers (C.81069, Fig. 31, and C.81070, Fig. 33) are preserved as rough internal casts and show no ornament except for the large ventrolateral and smaller umbilical tubercles and ribs connecting them. If adult, they would indicate maximum sizes of about 200 mm diameter, which is smaller than the maximum sizes attained by specimens in the type population in southern India. The strength of the tubercles and ribs is different in each fragment, and appears to show that there is considerable variation in these characters. The same species also occurs in north-east Brazil, where it was given the name *Ammonites pedroanus* White. The single specimen figured by both White (1887) and Maury (1936) is large and roughly preserved, and shows the characteristic prominent

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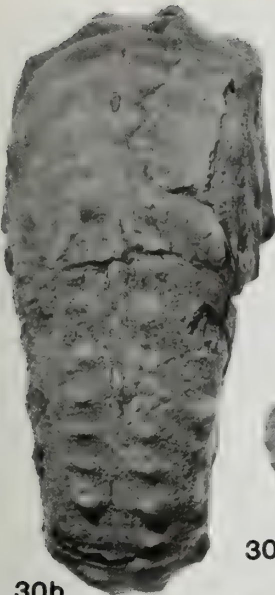
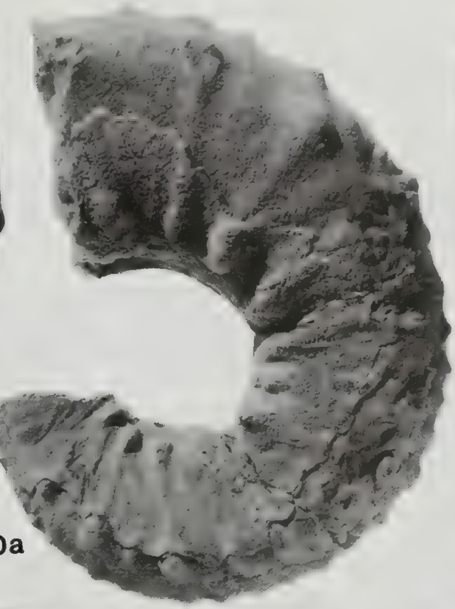
Figs 30–33 *Pseudaspidoceras footeanum* (Stoliczka) from Lower Turonian at loc. 1007. Fig. 30, C.81073, ×1; Fig. 31, C.81069, ×0·78; Fig. 32, C.81072, ×0·78; Fig. 33, C.81070, ×0·78.



30b



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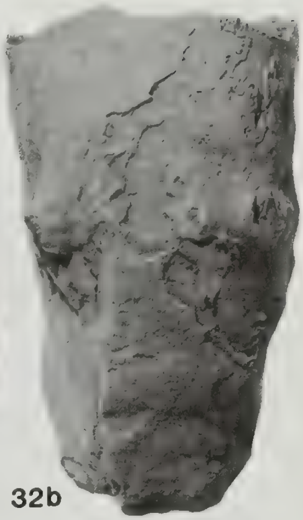

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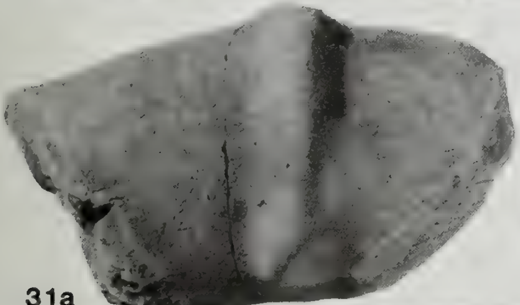

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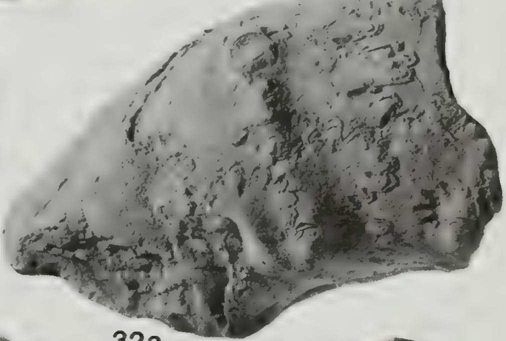

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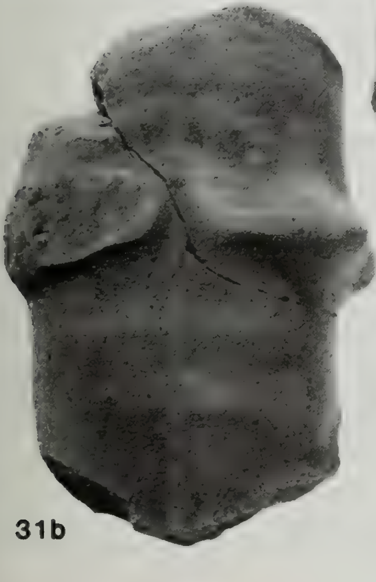

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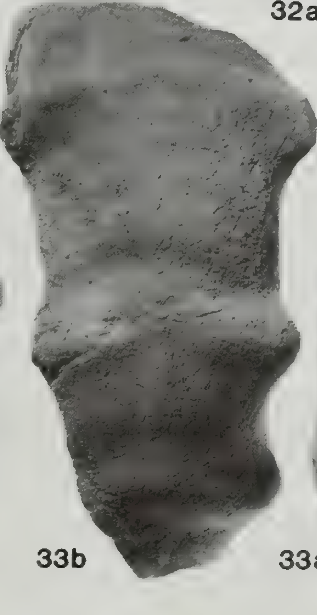

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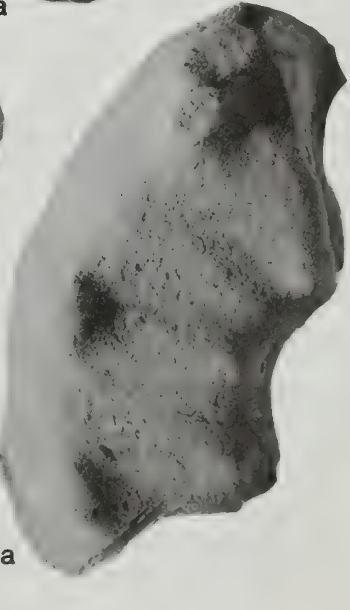

33a

tubercles and subordinate ribbing. Another similar specimen from Brazil was figured by Reyment & Tait (1972: pl. 3, fig. 12). White's specific name is considered here to be a synonym of *P. footeanum.* The species also occurs in Mexico and specimens have been figured by Böse (1918) and Chancellor, Reyment & Tait (1978) (see synonymy), but the large example from Germany figured by Petrascheck (1902: 144; pl. 9, fig. 1) as *P. footeanum* is considerably more compressed and belongs to *P. flexuosum* (Powell).

OCCURRENCE. This species occurs in the Lower Turonian of England, India, Israel (Freund & Raab 1969: 14), Brazil, Mexico and Angola.

Family **VASCOCERATIDAE** H. Douvillé, 1912

Genus ***VASCOCERAS*** Choffat, 1898

TYPE SPECIES. *Vascoceras gamai* Choffat, 1898.

Subgenus ***PARAVASCOCERAS*** Furon, 1935

TYPE SPECIES. *Vascoceras cauvini* Chudeau, 1909.

Vascoceras (Paravascoceras) harttii (Hyatt)

Fig. 25

1870 *Ceratites harttii* Hyatt: 386.
1875 *Buchiceras hartti* (Hyatt) Hyatt: 370.
1887 *Ammonites (Buchiceras) hartti* (Hyatt); White: 226; pl. 19, figs 1, 2; pl. 20, fig. 3.
1903 *Vascoceras hartti* (Hyatt): 103; pl. 14, fig. 16.
1925 *Vascoceras hartti* (Hyatt); Maury: 594–5.
1930 *Vascoceras hartti* (Hyatt); Maury: 280–3.
1936 *Vascoceras hartti* (Hyatt); Maury: 247; pl. 22, figs 1, 2.
1969 *Pachyvascoceras hartti* (Hyatt) Oliveira & Brito: 220; pl. 2, figs 1, 2 (*non* fig. 3, = *Fagesia*, *vide* Bengtson, 1983: 15).
non 1972 *Pachyvascoceras hartti* (Hyatt); Reyment & Tait: pl. 15, figs 26a–c (= *Fagesia, vide* Bengtson, 1983: 15).
1978 *Paravascoceras hartti* (Hyatt) Chancellor, Reyment & Tait: 96; fig. 20.
1983 *Paravascoceras hartti* (Hyatt); Bengtson: 15.

MATERIAL. Two specimens, C.81075–6, from loc. 1007.

MEASUREMENTS.	D	Wh	Wb	U
C.81075	88·0	33·5 (0·38)	75 (0·85)	25·2 (0·29)
	68·0	28·2 (0·41)	64 (0·94)	19·0 (0·28)

DESCRIPTION. The specimens have maximum diameters of 88 mm and 60 mm respectively, and both are septate up to the aperture. Both are well-preserved, with much of the shell intact. The larger specimen has part of its venter worn away on its final quarter whorl, while the smaller specimen has both sides worn away for most of the final half whorl. The whorls are moderately involute, globose and cadicone, and have a highly depressed whorl section. The whorl breadth/ whorl height ratio of the larger specimen is 2·25, and the smaller specimen appears to be similarly highly depressed. (Whorl height is the height measured between the line joining the umbilical seams and the centre of the venter. It is not the height from the centre of the dorsum to the centre of the venter, which is significantly smaller.) The umbilical wall is nearly vertical on the inner whorls and steeply inclined on the outer whorl, and leads to a smoothly rounded umbilical edge. The venter is broadly arched and is very slightly angled along the centre line. The shell is smooth, with neither ribs nor tubercles present from the smallest size visible, which is about 25 mm diameter. Suture-lines are not visible in detail.

DISCUSSION. These two cadicone, globose and highly depressed Angolan specimens are without any ornament at sizes between 20 mm and 90 mm diameter, and match the Brazilian type specimen of Hyatt's species exactly. Other smooth cadicone specimens of the species are known from Brazil (Oliveira & Brito 1969) and from Coahuila, Mexico (Chancellor, Reyment & Tait 1978). The large amount of intraspecific variation in whorl proportions and ornament has led to many different views on the generic classification of Vascoceratidae. Possible generic determinations for this smooth cadicone species are *Vascoceras*, *Pachyvascoceras* and *Paravascoceras* as full genera, or with the latter two as subgenera of *Vascoceras*. The view adopted here, that *harttii* is a species of *Vascoceras* (*Paravascoceras*), follows the views of Freund & Raab (1969) and Schöbel's (1975) analysis of the Niger population of Vascoceratidae, though *Paravascoceras* is preferred as a subgenus rather than a full genus because of its close connexion with *Vascoceras*. The Portuguese species *Vascoceras harttiforme* (Choffat 1898: 61; pl. 12, fig. 3; pl. 13, figs 3–6; pl. 21, figs 22–4) is hardly different from *V.* (*P.*) *harttii*, and the stratigraphical analysis of Lauverjat & Berthou (1974: 269; table p. 292) has shown that the bed in which it occurs (division L) is at the top of the Lower Turonian. It belongs to 'group iv' (involute, cadicone, unornamented) of Berthou, Brower & Reyment (1976: 76), which is the youngest group of Vascoceratidae to develop in the Portuguese Turonian.

OCCURRENCE. This species occurs in the Lower Turonian of Angola, north-east Brazil and Mexico.

References

Anderson, F. M. 1958. Upper Cretaceous of the Pacific Coast. *Mem. geol. Soc. Am.*, Washington, **71.** xi + 378 pp., 75 pls.

Benavides-Cáceres, V. E. 1956. Cretaceous system in northern Peru. *Bull. Am. Mus. nat. Hist.*, New York, **108:** 353–494, pls 31–66.

Bengtson, P. 1983. The Cenomanian–Coniacian of the Sergipe Basin, Brazil. *Fossils Strata*, Oslo, **12:** 1–78.

Berthou, P. Y., Brower, J. C. & Reyment, R. A. 1976. Morphometrical study of Choffat's vascoceratids from Portugal. *Bull. geol. Instn Univ. Upsala,* (n.s.) **6:** 73–83.

Böse, E. 1918. On a new ammonite fauna of the Lower Turonian of Mexico. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **1856:** 173–252.

—— 1928. Cretaceous ammonites from Texas and northern Mexico. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **2748** (for 1927): 143–312, pls 1–18.

Boule, M., Lemoine, P. & Thévenin, A. 1906–07. Paléontologie de Madagascar. III – Céphalopodes crétacés des environs de Diègo-Suarez. *Annls Paléont.*, Paris, **1:** 173–192, pls 14–20 (1906); **2:** 1–56, pls 1–8 (1907).

Breistroffer, M. 1933. Étude de l'étage Albien dans le Massif de la Chartreuse (Isère et Savoie). *Trav. Lab. Géol. Univ. Grenoble,* **17** (3): 1–50.

Chancellor, G. R. C., Reyment, R. A. & Tait, E. A. 1978. Notes on Lower Turonian ammonites from Loma el Macho, Coahuila, Mexico. *Bull. geol. Instn Univ. Upsala,* (n.s.) **7:** 85–101.

Choffat, P. 1898. Recueil d'ètudes paléontologiques sur la faune crétacique du Portugal. **1.** Espèces nouvelles ou peu connues. 2, Les ammonées du Bellasien, des Couches à *Neolobites Vibrayeanus,* du Turonien et du Sénonien. *Mém. Commn. géol. Port.*, Lisbon, **1898:** 41–86, pls 3–22.

Cobban, W. A. 1971. New and little known ammonites from the Upper Cretaceous (Cenomanian and Turonian) of the Western Interior of the United States. *Prof. Pap. U.S. geol. Surv.*, Washington, **699.** 24 pp., 18 pls.

—— **& Scott, G. R.** 1972. Stratigraphy and ammonite fauna of the Graneros Shale and Greenhorn Limestone near Pueblo, Colorado. *Prof. Pap. U.S. geol. Surv.*, Washington, **645.** 108 pp., 41 pls.

Collignon, M. 1928–29. Les céphalopodes du Cénomanien pyriteux de Diègo-Suarez, Paléontologie de Madagascar. *Annls Paléont.*, Paris, **17:** 139–160, pls 15–19 (1928); **18:** 1–56, pls 1, 2 (1929).

—— 1931. La faune du Cénomanien à fossiles pyriteux du nord de Madagascar. *Annls Paléont,* Paris, **20:** 43–104, pls 5–9.

—— 1933. Fossiles Cénomaniens d'Antsatramahavelona (Province d'Analalava, Madagascar). *Annls géol. Surv. Mines Madagascar,* Tananarive, **3:** 53–79, 6 figs, pls 5, 6.

—— 1964–65. *Atlas des fossiles caractéristiques de Madagascar* (*Ammonites*). **XI** (Cénomanien). xi + 152 pp., pls 318–375 (1964). **XII** (Turonien). iv + 82 pp., pls 376–413 (1965). Service géologique, Tananarive.

—— 1978. Ammonites du Cretacé moyen-supérieur de l'Angola. In: *Reconhecimento científico de Angola: Estudos de Geologia e Paleontologia e de Micologia.* 75 pp., 32 pls. Lisbon (II Centenário da Academia das Ciencias de Lisboa).

Cooper, M. R. 1973. Cenomanian ammonites from Novo Redondo, Angola. *Ann. S. Afr. Mus.*, Cape Town, **62:** 41–67, figs 1–13.

—— 1978*a*. Uppermost Cenomanian–basal Turonian ammonites from Salinas, Angola. *Ann. S. Afr. Mus.*, Cape Town, **75** (5): 51–152.

—— 1978*b*. The mid-Cretaceous (Albian–Turonian) biostratigraphy of Angola. *Annls Mus. Hist. nat. Nice*, **4:** XVI.1–22, 6 pls.

—— **& Kennedy, W. J.** 1979. Uppermost Albian (*Stoliczkaia dispar* Zone) ammonites from the Angolan littoral. *Ann. S. Afr. Mus.*, Cape Town, **77** (10): 175–308.

Cragin, F. W. 1893. A contribution to the invertebrate paleontology of the Texas Cretaceous. *Rep. geol. Surv. Texas*, Austin, **4** (1892): 139–246, pls 24–46.

Douvillé, F. 1904. Paléontologie, mollusques fossiles. *In* Morgan, J. de, *Mission scientifique en Perse* **3** (4): 191–380, pls 25–50. Paris.

—— 1931. Contribution à la géologie de l'Angola. Les ammonites de Salinas. *Bolm Mus. Lab. miner. geol. Univ. Lisb.*, **1:** 17–46, pls 1–4.

Förster, R. 1975. Die geologische Entwicklung von Süd-Mozambique seit der Unterkreide und die Ammoniten-Fauna von Unterkreide und Cenoman. *Geol. Jb.*, Hannover, (B) **12:** 3–324, pls 1–17.

Freund, R. & Raab, M. 1969. Lower Turonian ammonites from Israel. *Spec. Pap. Palaeont.*, London, **1.** v + 83 pp., 10 pls.

Haas, O. 1942. Some Upper Cretaceous ammonites from Angola. *Am. Mus. Novit.*, New York, **1182:** 1–24.

—— 1952. Some Albian desmoceratid and lytoceratid ammonites from Angola. *Am. Mus. Novit.*, New York, **1561:** 1–17.

Haughton, S. H. 1930. On the occurrence of Upper Cretaceous marine fossils near Bogenfels, S. W. Africa. *Trans. R. Soc. S. Afr.*, Cape Town, **18:** 361–365, pl. 11.

Howarth, M. K. 1965. Cretaceous ammonites and nautiloids from Angola. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **10** (10): 335–412, 13 pls.

—— 1968. A mid-Turonian ammonite fauna from the Moçamedes desert, Angola. *Garcia de Orta*, Lisbon, **14:** 217–228, pls 1–3.

Hyatt, A. 1870. Report on the Cretaceous fossils from Mariom. *In* Hartt, C. F., *Geology and physical geography of Brazil:* 385–393. Boston.

—— 1875. The Jurassic and Cretaceous ammonites collected in S. America by Prof. James Orton, with an appendix upon the Cretaceous ammonites of Prof. Hartt's collection. *Proc. Boston Soc. nat. Hist.*, **17:** 365–378.

—— 1903. Pseudoceratites of the Cretaceous. *Monogr. U.S. geol. Surv.*, Washington, **44.** 351 pp., 47 pls.

Kellum, L. B. & Mintz, L. W. 1962. Cenomanian ammonites from the Sierra de Tlahualilo, Coahuila, Mexico. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **13:** 267–287, pls 1–8.

Kennedy, W. J. 1971. Cenomanian ammonites from southern England. *Spec. Pap. Palaeont.*, London, **8.** v + 133 pp., 64 pls.

—— **& Hancock, J. M.** 1977. Towards a correlation of the Cenomanian sequences of Japan with those of north-west Europe. *Spec. Pap. palaeont. Soc. Japan*, Tokyo, **21:** 127–141.

—— —— 1978. The mid-Cretaceous of the United Kingdom. *Annls Mus. Hist. nat. Nice*, **4:** V.1–72, 30 pls.

—— **& Klinger, H. C.** 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **25** (4): 263–315, 1 pl., 12 text-figs.

—— —— 1977. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Phylloceratidae. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **27** (5): 347–380, 15 pls, 9 text-figs.

Klinger, H. C. & Kennedy, W. J. 1978. Turrilitidae (Cretaceous Ammonoidea) from South Africa, with a discussion of the evolution and limits of the family. *J. molluscan Stud.*, London, **44:** 1–48, 9 pls.

Kossmat, F. 1895. Untersuchungen über die Südindische Kreideformation. *Beitr. Paläont. Geol. Öst-Ung.*, Vienna, **9** (3–4): 97–203, pls 15–25.

Lapao, L. G. P. 1972. Novo Redondo. *Província de Angola. Carta geológica*, 1:100.000, Folha no. **184.** 1 map + 58 pp. Luanda.

Lauverjat, J. & Bertou, P. Y. 1974. Le Cénomano-Turonien de l'embouchure du Rio Mondego, Beira Littoral, Portugal. *Comunções Servs geol. Port.*, Lisbon, **57:** 263–301, 13 pls.

Mantell, G. A. 1822. *The fossils of the South Downs; or Illustrations of the geology of Sussex.* xvii + 327 pp., 42 pls. London.

Matsumoto, T. 1942. A note on the Japanese Cretaceous ammonites belonging to the subfamily Desmoceratinae. *Proc. Imp. Acad. Japan*, Tokyo, **18:** 24–29.

—— 1954. Appendix. Selected Cretaceous leading ammonites in Hokkaido and Saghalien. *In* Matsumoto,

T. (Ed.), *The Cretaceous System in the Japanese Islands:* 243–313, pls 17–36. Jap. Soc. Promotion Sci., Tokyo.

—— 1959. Upper Cretaceous ammonites of California. Part II. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **Spec. vol. 1**. 172 pp., 41 pls.

—— **& Miller, H. W., jr** 1958. Cretaceous ammonites from the spillway excavation of Cedar Bluff Dam, Trego County, Kansas. *J. Paleont.*, Tulsa, **32:** 351–356, pls 44–5.

——**, Muramoto, T. & Takahashi, I.** 1969. Selected acanthoceratids from Hokkaido. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **19:** 251–296, pls 25–38.

Maury, C. J. 1925. Fosseis terciaros do Brasil, com descripção de novas formas cretaceas. *Monografias Serv. geol. miner. Bras.*, Rio de Janeiro, **4.** 705 pp., 24 pls.

—— 1930. O Cretaceo da Parahyba do Norte. *Monografias Serv. geol. miner. Bras.*, Rio de Janeiro, **8.** 305 pp., 35 pls.

—— 1936. O Cretaceo de Sergipe. *Monografias Serv. geol. min. Bras.*, Rio de Janeiro, **11.** 283 pp., 28 pls.

Meek, F. B. 1876. *In* Meek, F. B. & Hayden, F. V., A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country. *Rep. U.S. geol. geogr. Surv. Territ.*, Washington, **9.** lxiv + 629 pp., 45 pls.

Moreman, W. L., 1927. Fossil zones of the Eagle Ford of north Texas. *J. Paleont.*, Chicago, **1:** 89–101, pls 13–16.

—— 1942. Paleontology of the Eagle Ford group of north and central Texas. *J. Paleont.*, Tulsa, **16:** 192–220, pls 31–34.

Oliveira, P. E. & Brito, I. M. 1969. Amonitas Turonianos do Estado de Sergipe. *Anais Acad. bras. Cienc.*, Rio de Janeiro, **41:** 215–233, pls 1–5.

Passy, A. 1832. *Description géologique du department de la Seine-inférieure.* 371 pp., 20 pls. Rouen.

Pervinquière, L. 1907. *Carte géologique de la Tunisie. Études de paléontologie tunisienne,* **1.** Céphalopodes des terrains secondaires. 438 pp., 27 pls. Paris.

—— 1910. Sur quelques ammonites du Crétacé Algérien. *Mem. Soc. géol. Fr. Paléont.*, Paris, **42.** 86 pp., 7 pls. (**17** (2–3): f. 8–18, pls 10–16.)

Petrascheck, W. 1902. Die Ammoniten der sächsischen Kreideformation. *Beitr. Paläont. Geol. Ost.-Ung.*, Vienna, **14:** 131–162, pls 7–12.

Powell, J. D. 1963. Cenomanian–Turonian (Cretaceous) ammonites from trans-Pecos Texas and northeastern Chihuahua, Mexico. *J. Paleont.*, Menasha, **37:** 309–322, pls 31–34.

Reeside, J. B. & Weymouth, A. A. 1931. Mollusks from the Aspen Shale (Cretaceous) of southwestern Wyoming. *Proc. U.S. natn. Mus.*, Washington, **78** (17): 1–24, pls 1–4.

Renz, O. 1982. *The Cretaceous ammonites of Venezuela.* 132 pp., 40 pls. Basel, Boston, Stuttgart.

Reyment, R. A. 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria,* Kaduna, **25.** 112 pp., 25 pls.

—— **& Tait, E. A.** 1972. Biostratigraphical dating of the early history of the South Atlantic Ocean. *Phil. Trans. R. Soc.*, London, (B) **264:** 55–95, pls 3–5.

Schlüter, C. 1871. Die Cephalopoden der oberen deutschen Kreide (part 1). *Palaeontographica,* Stuttgart, **21:** 1–24, pls 1–18.

Schöbel, J. 1975. Ammoniten der Familie Vascoceratidae aus dem Unteren Unterturon des Damergou-Gebietes, République du Niger. *Spec. Vol. Palaeont. Inst. Univ. Uppsala,* **3.** 136 pp., 6 pls.

Sharpe, D. 1853. Description of the fossil remains of Mollusca found in the Chalk of England. **1,** Cephalopoda (part 1): 1–26, pls 1–10. *Palaeontogr. Soc.* (*Monogr.*), London.

Spath, L. F. 1925. On Upper Albian Ammonoidea from Portuguese East Africa. With an appendix on Upper Cretaceous ammonites from Maputoland. *Ann. Transv. Mus.*, Pretoria, **11:** 179–200, pls 28–37.

Stanton, T. W. 1894. The Colorado formation and its invertebrate fauna. *Bull. U.S. geol. Surv.*, Washington, **106.** 288 pp., 45 pls.

Stoliczka, F. 1864. The fossil Cephalopoda of the Cretaceous rocks of southern India. Ammonitidae with revision of the Nautilidae &c. *Mem. geol. Surv. India Palaeont. indica,* Calcutta, (3) **2–5:** 57–106, pls 32–54.

White, C. A. 1887. Contribuicoes á paleontologia do Brazil. *Archos Mus. nac. Rio de J.*, **7:** 1–273, 28 pls.

Wiedmann, J. 1962*a*. Die systematische Stellung von *Hypophylloceras* Salfeld. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, (A) **115:** 243–256, pl. 16.

—— 1962*b*. Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1, Phylloceratina, Lytoceratina. *Palaeontographica,* Stuttgart, (A) **118:** 119–237, pls 8–14.

—— 1964. Unterkreide-Ammoniten von Mallorca, 2. Lieferung: Phylloceratina. *Abh. math.-naturw. Kl. Akad. Wiss. Mainz,* Jahr. **1963** (4): 157–264, pls 11–21.

—— **& Dieni, I.** 1968. Die Kreide Sardiniens und ihre Cephalopoden. *Palaeontogr. ital.*, Pisa: **64:** 1–171, 18 pls.

Wolleben, J. A. 1967. Senonian (Cretaceous) Mollusca from Trans-Pecos Texas and northeastern Chihuahua, Mexico. *J. Paleont.*, Tulsa, **41:** 1150–1165, pls 147–152.

Wright, C. W. 1963. Cretaceous ammonites from Bathurst Island, Northern Australia. *Palaeontology*, London, **6:** 597–614, pls 81–89.

—— **& Kennedy, W. J.** 1981. The Ammonoidea of the Plenus Marls and the Middle Chalk. 148 pp., 32 pls. *Palaeontogr. Soc.* (*Monogr.*), London.

—— —— 1984. The Ammonoidea of the Lower Chalk (part 1): 1–126; pls 1–40. *Palaeontogr. Soc.* (*Monogr.*), London.

Young, K. 1958. Cenomanian (Cretaceous) ammonites from Trans-Pecos Texas. *J. Paleont.*, Tulsa, **32:** 286–294, pls 39–40.

—— **& Powell, J. D.** 1978. Late Albian–Turonian correlations in Texas and Mexico. *Annls Mus. Hist. nat. Nice*, **4:** XXV.1–39, 9 pls.

Index

Page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

Acanthoceras 93
  borgesi 93
  kanabense 93
  laticlavium 86
  meridionale 93
  (*Mantelliceras*) *falloti* 86
Acanthocerataceae 85–101
Acanthoceratidae 86–100
Acanthoceratinae 93
Acutus Zone 76
Adkins, W. S. 85
Africa 82, 86, 97
  north 81, 95
  south-east 85
Albian 74–5, 78, 82
Ammonites euomphalus 93
  footeanus 97–8
  largilliertianus 85
  laticlavius 86
  latidorsatus 82
  meridionalis 93
  navicularis 91
  obtectus 86
  pedroanus 98
  (*Buchiceras*) *hartti* 100
Ammonitina 82–101
Ancyloceratina 79–82
Aptian 74, 79
Asia 86
Australia 95

Benguela 75*
Brazil 98, 100–1
British Museum (Natural History) 78
Britton Formation 78, 85
Buchiceras hartti 100

California 84
Calycoceras (*C.*) 77, 91–3
  naviculare 74, 77, **91–3,** 92*; Zone 77
Campanian 85
Carcitanensis Zone 76
Cenomanian 74–5
  Lower 76–9, 81, 86–7
  Middle 77, 79, 81–2, 86
  Upper 77–8, 82, 85, 97
Ceratites harttii 100
Coahuila 101
Costatus zone 76
Cretaceous 74; see Cenomanian, &c.
Cuanza 74

Desmoceras (*D.*) 82–4
  kossmati 82, 84
  latidorsatum 82, 84
    inflatum 84
    lemoinei 74, 76, **82–4,** 83*
    perinflatum 84
  lemoinei 84
  (*Latidorsella*) *latidorsata* 82
    lemoinei 82
  (*Pseudouhligella*) *elgini* 82, 84
Desmocerataceae 82–4
Desmoceratidae 82–4

Eagle Ford Group 85
England 78, 84, 88, 100
Euomphaloceras 74, 76, **93,** 94–7
  (*E.*) 93
    cunningtoni 74, 76, 95
      var. *meridionale* 77, 92*, **93–5,** 94*
    euomphalus 93, 97
    meridionale 93
    septemseriatum 95
  (*Kanabiceras*) 93, 95–7
    septemseriatum 74, 77, 93, **95–7,** 96*
Euomphaloceratinae 93–7
Europe 78, 82, 85, 97
Exogyra 85

Fagesia 100
Forbesiceras 74, 85–6
  largilliertianum 85
  obtectum 74, 76, 83*, **86**
Forbesiceratidae 85–6
France 95

Gaudryceras sp. indet. 76
Germany 100
Geslinianum Zone 77–8
Graysonites byzenica 91

Hoplitaceae 84–5
Hyporbulites, see *Phylloceras*
Hypophylloceras, see *Phylloceras*

India 78, 95, 100
Israel 78, 100

Japan 84, 88, 95, 97
Juddii Zone 77

Kamerunoceras 93
Kanabiceras 95–7; see *Euomphaloceras*
  kanabense 95
  septemseriatum 95, 97

Latidorsella, see *Desmoceras*
Luanda 74, 75*, 88
Lyelliceras stanislausense 95

Madagascar 79, 81–2, 85, 88, 95
Mammites 97–8
  mocamadensis 98
Mammitinae 97–100
Mantelliceras 86; see *Acanthoceras*
  falloti 86
  laticlavium var. *mexicanum* 88
Mantelliceratinae 86–93
Mariella (*M.*) 74
  oehlerti 76, **79–81,** 80*
    sulcata 81
Mexico 88, 100–1
Moçamedes 74, 75*
Mozambique 79, 88

Namibia 85
Naviculare Zone 77
Neocardioceras septemseriatum 75
Niger 101
North America 82, 88, 97; see Texas, California

Novo Redondo 74, 75*, 76–7, 81, 86, 95

Obiraceras 93
Ostlingoceras (*O.*) 74, 79
  puzosianus 79
  cf. *rorayense* 76, **79,** 80*

Pachyvascoceras 101
  hartti 100
Paravascoceras 100–1; see *Vascoceras*
  hartti 100
Peru 88
Phylloceras 78–9
  onoense 78
  velledae var. *seresitense* 78
  (*Hyporbulites*) *seresitense seresitense* 78
  (*Hypophylloceras*) **78–9**
    onoense 78
    seresitense 76–7, **78–9,** 80*
Phylloceratidae 78–9
Phylloceratina 78–9
Placenticeras 85
  fritschi 84
  intercalare 84
  merenskyi 84–5
  stantoni var. *bolli* 84
Placenticeratidae 84–5
Pleistocene 75
Portugal 78, 101
Pre-Cambrian 74
Prionotropis echinatus 95
Proplacenticeras 78, 84–5
  cumminsi 85
  fritschi 84
  memoriaschloenbachi 85
    var. *ambiloensis* 84
  orbignyanum 85
  pseudoplacenta (cf.) 85
    var. *occidentale* 85
  stantoni 74
    var. *bolli* 77–8, 80*, **84–5**
Pseudaspidoceras **97,** 98–100
  flexuosum 100
  footeanum 74, 77–8, 97, **98–100,** 99*
  pedroanum 98
Pseudoaspidoceras, see *Pseudaspidoceras*
Pseudouhligella, see *Desmoceras*
Puzosia sp. indet. 76

Recent 75
Romaniceras 93

Salinas 74, 97
Scaphites septemseriatum 95
Schindewolfites 93
Senonian 75
Sharpeiceras 74, 76, **86,** 87–91
  falloti 88
  florencae 74, 76, **86–8,** 87*, 89*, 90*, 91
  goliath 86, 88
  kongo 88
  laticlavium 86, 88, 91
    var. *indica* 88, 91
  mexicanum 76, **88–91,** 90*, 92*
  occidentale 86, 88
  schlueteri 86, 88, 91
  vohipalense 86
Shuparoceras 93

Texas 78, 84–5, 95
Tlahualitoceras tlahualitoense 86, 88
Turonian 74–5, 85
  Lower 77–8, 85, 97, 100–1
Turrilitaceae 79–82
Turrilites 74, 81–2
  acutus 76, 80*, **81–2;** Zone 76
  bergeri 79
  costatus 81; Zone 76
  gresslyi 79
  oehlerti 79
  puzosianus 79
  rorayensis 79
Turrilitidae 76, 79–82

Vascoceras 78, 100–1
  cauvini 100
  gamai 100
  harttiforme 101
  (*Paravascoceras*) *cauvini* 100
    hartti 100
    harttii 74, 77–8, 95*, 100–1
Vascoceratidae 100–1
Venezuela 88

Woolgari Zone 85

Yubariceras 93

Zululand 79, 81–3, 88

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British Museum (Natural History)

The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

B. G. Gardiner

There are some 25,000 species of actinopterygians, far out-numbering the tetrapods and accounting for over half of all the living species of vertebrates. The Actinopterygii contain such diverse forms as polypterids, sturgeons, paddle fishes, gars, the bowfin and the enormous variety of teleosts. The Devonian actinopterygians described in this monograph stand near the base of the Osteichthyes, a natural group including the coelacanths, lungfishes and tetrapods.

This unique Upper Devonian fish fauna was discovered in 1963 by Mr Harry Toombs of the British Museum (Natural History) while on a collecting trip to Australia. The majority of the material was subsequently collected in 1967 by a joint expedition from the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow.

The discovery of these superbly preserved Devonian palaeoniscids at Gogo, Western Australia, has not only greatly increased our knowledge of the early actinopterygian condition but has also enabled us to appreciate the original osteichthyan plan. In other words, many of the characters of the Gogo palaeoniscids are primitive for all bony fishes, and this in turn allows comparison with the other gnathostome groups. These Devonian species also provide detailed information which illuminates many problems in the structure and evolution of the actinopterygians. This knowledge has permitted a more comprehensive and soundly based account of the history of that group.

The relationships are expressed in a new classification of gnathostomes in which the placoderms are considered to be the sister-group of the osteichthyans, the acanthodians the sister-group of those two and the chondrichthyans the primitive sister-group of other gnathostomes. The Porolepiformes are considered to be the sister-group of the choanates.

Finally the interrelationships of actinopterygians are reviewed and the great range of fossil forms presently included in the Palaeonisciformes discussed.

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The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England

P. E. S. Whalley

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The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England

P. E. S. Whalley

Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis 107
Introduction 108
Geology, preservation and techniques 109
Check-list of insects from the Dorset Lias 110
Survey of Insect Orders from the Dorset Lias 111
Systematic section 113
  Blattodea, cockroaches 113
  Dermaptera, earwigs 116
  Odonata, dragonflies 117
  Orthoptera, grasshoppers and crickets 126
  Phasmatodea, stick-insects 137
  Hemiptera, plant bugs 140
  Raphidioptera, snakeflies 147
  Mecoptera, scorpion flies 150
  Diptera, two-winged flies 157
  Lepidoptera, butterflies and moths 159
  Coleoptera, beetles 164
Discussion 176
Comparison with other Mesozoic faunas 181
Palaeogeography 182
Phylogeny 183
Acknowledgements 184
References 184
Index 187

Synopsis

Over 400 Lower Liassic insect fossils collected in Dorset, England, have been studied. These include 66 species in over 30 genera of which 11 new genera and 21 new species are described and their relationships discussed. Several families of insects are recorded for the first time in Britain, while the Orders Dermaptera (earwigs), Phasmatodea (stick-insects) and a scale-covered lepidopterous insect are recorded for the first time in the Lower Lias.

The following new taxa are proposed: *Nannoblattina petulantia* sp. nov. (Blattodea); *Brevicula gradus* gen. et sp. nov. (Dermaptera); *Liassophlebia pseudomagnifica* sp. nov., *Hypsothemis fraseri* sp. nov. and *Dorsettia laeta* gen. et sp. nov. (Odonata); *Archelcana durnovaria* sp. nov., *Orichalcum ornatum* gen. et sp. nov., *Regiata scutra* gen. et sp. nov. and *Micromacula gracilis* gen. et sp. nov. (Orthoptera); *Durnovaria parallela* gen. et sp. nov. (Phasmatodea); *Paraprosbole rotruda* gen. et sp. nov. and *Mesocixiella* (?) *fennahi* sp. nov. (Hemiptera–Homoptera); *Metaraphidia confusa* gen. et sp. nov. and *Priscaenigma obtusa* gen. et sp. nov. (Raphidioptera); *Orthophlebia capillata* sp. nov. and *Pseudopolycentropus prolatipennis* sp. nov. (Mecoptera); *Prodocidia spectra* gen. et sp. nov. (Diptera); *Archaeolepis mane* gen. et sp. nov. of new family Archaeolepidae (Lepidoptera); *Elaterophanes regius* sp. nov., *Liassocupes* (?) *maculatus* sp. nov. and *L.* (?) *giganteus* sp. nov. (Coleoptera). Eight new species of Hemiptera–Heteroptera are placed in open nomenclature.

A survey of the fauna is used to consider the environment from which the insects were derived. The Dorset insects are compared with other British and continental Mesozoic insect faunas. The palaeogeography of the Sinemurian (Lower Lias) of south-west Britain is considered and a new assessment of the distribution of the land masses is postulated based on the data derived from the fossil insects.

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Introduction

> *The complete description of the [insect] fauna from Charmouth will require considerable time, partly because the poor state of preservation imposes a heavy strain on the eyes of the investigator, and partly because the fragments require large-scale comparison with more complete material from a great variety of insect orders.* F. E. Zeuner (1962: 160)

Fossil insects are particularly well represented in the British Jurassic and were extensively collected by the Rev. P. B. Brodie who published his classic work, *The History of the Fossil Insects in the Secondary Rocks of England*, in 1845. Various authors on the continent of Europe (Giebel 1856, Handlirsch 1906–08) or in North America (Scudder 1886) have described insects from the British Mesozoic.

The present study is based almost entirely on a remarkable collection of insect fossils from the Dorset Lias made by James Frederick Jackson (1894–1966). His collection was purchased over a period of years by the British Museum (Natural History) (Zeuner 1962: 155). Jackson first published on Dorset coastal geology in 1926 but his other published works dealt only with the geology of the Isle of Wight (Lang 1968). When, in 1951, Jackson moved to Charmouth (Dorset) he spent his retirement collecting fossils in the Lower Lias, not only insects but also ammonites, crinoids and other groups, all of which came to the Museum.

Gardiner (1961) was the first to publish a description of an insect from the Dorset Lias, which was discovered in the orbit of the eye of a fossil fish during its acid preparation.

Jackson's collection of fossil insects, which consists of 434 specimens, has however not previously been studied in its entirety. Some were published by Zeuner (1962), who studied 65 specimens from the collection, 43 of which belonged to one species of Coleoptera. Two other specimens from the Dorset Lias are also included in the present study, a snakefly (Raphidioptera) in the collection of the British Geological Survey and a waterbug (Hemiptera–Heteroptera) in that of the Bristol Museum and Art Gallery.

The study of these Dorset Lias fossils is part of a wider project on British Mesozoic insects. Many of the previously-described insect fossils from British localities are the types of genera, few have been studied since they were first described and many, with new techniques, can be developed further to reveal important characters not visible when they were originally examined.

When the Jackson collection was originally received at the Museum all the specimens were given register numbers as insect fossils. Some, however, on closer examination have proved to be fragments of plants or fish. When Zeuner studied the collection there were 434 specimens registered as insects and he based his percentages of the various orders (1962: 158) on this total. In fact 30 of the registered specimens are not insects and this was taken into account when the figures were calculated for the comparison in Table 1, in which the corrected figures more accurately reflect the fossil fauna. The main discrepancies are in the Hemiptera, where Zeuner's figure for the total was too low, probably because he included some of them in his category 'cannot be classified without further detailed work', and the same is probably true of his figure for the Panorpoid complex, in which he included the Diptera, Mecoptera, and Neuroptera (i.e. Raphidioptera herein), but here the discrepancy is smaller.

Whilst all the insect orders present greater or lesser problems of identification and interpretation, the problem of identification of the Coleoptera has proved intractable (p. 164). Beetles form over 39% of the total insects and this high percentage reflects not only their persistence as fossils but also gives an indication of their original abundance. It is almost impossible to classify isolated Mesozoic beetle elytra to Recent families, because of the virtual absence of wing venation, which is used for identification in many insect groups especially amongst fossils, although in some cases a reasonable guess can be made. But when more detailed studies of Mesozoic beetles have been made, it may be possible to build up a closer association with Recent families similar to the one developed by Coope (e.g. Coope 1979) for Pleistocene beetles. In the present study a few readily recognizable and more complete beetle fossils are associated with Recent families, the rest being placed in numbered species-groups consisting of similar and probably related insects associated by size, shape and sculpturing of the elytra. This allows a rough estimate to be made of the diversity of the beetle fauna.

Table 1 Numbers of insects in Jackson collection, and percentages of each order. A – number of specimens in Jackson collection. B – percentage. C – insects from other collections included in the present study. D – Zeuner's (1962) estimate, with corrected percentage figures (a, Hemiptera; b, 'Panorpoid complex', see p. 108). Zeuner's figures have been corrected for the actual insect total and these should be used with his 1962 paper. The total number of registered specimens in the Jackson collection is 434.

	A	B	C	D
Blattodea	6	1·5	–	1·9
Dermaptera	2	0·5	–	–
Odonata	10	2·5	–	2·7
Orthoptera	83	20·6	–	22·3
Phasmatodea	1	0·2	–	–
Homoptera	5	1·2	–	2·7^{a}
Heteroptera	29	7·2	1	
Raphidioptera	1	0·2	1	3·4^{b}
Mecoptera	15	3·7	–	
Diptera	1	0·2	–	
Lepidoptera	1	0·2	–	–
Coleoptera	160	39·6	–	40·9
Indeterminate insects	90	22·5	–	26·1
Total insects	404		2	
Non-insect fragments	30		–	

Zeuner (1962: 159) mentioned a 'solitary Hymenopteron (*sic*) of the sawfly type' in the Jackson collection but does not elaborate on this statement. In spite of careful examination this specimen has not been found: in fact no Hymenoptera were found amongst the 404 insect specimens in the Jackson collection.

The descriptions of the Dorset Hemiptera–Heteroptera will be included in a joint publication on British Mesozoic Heteroptera by W. R. Dolling (British Museum (Natural History)), Y. A. Popov (Institute of Palaeontology, Moscow) and the author. This was to have been published before the present study but has been delayed; only a summary of the Dorset Heteroptera is included here.

Although many of the insects are well preserved, or represent an extension of our knowledge of the Order in distribution or time, probably one of the most remarkable fossils is the *Archaeolepis* (p. 159), showing the preservation of wing-scales very similar to those on the wings of Recent Lepidoptera.

Apart from the information afforded on morphology and the earlier occurrence of many groups than was previously known, the results of this study can be used to interpret the position of land masses in the Jurassic. Information about the extensive terrestrial fauna can also be used to evaluate the possible plant communities on the land from which the insects were derived.

Geology, preservation and techniques

Davis (1956, reprinted 1970) gave a general account of the geology of the Dorset coast; details of the rocks from which the fossil insects were obtained were given by Lang, Spath & Richardson (1923) and Lang & Spath (1926). A recent account of the zonation and correlation of these rocks can be found in Cope *et al.* (1981: 35, fig. 5a).

The insect fossils were mostly collected from the calcareous Flatstones and the Woodstone (parts of bed 83) in the Obtusum Zone (Upper Sinemurian); a few were found in the older

Turneri Zone in the Birchi Nodules (bed 75a, Lower Sinemurian). All are from a relatively short stretch of cliff at Charmouth, Dorset. Many are associated with ammonites (Figs 18, 27, 45) and four species of ammonites and four fish were mentioned by Zeuner (1962). Some of the insects are so closely associated with the ammonites that they must have been buried at the same time, in fact the wing of one of the dragonflies is literally wrapped around an ammonite (Fig. 8; p. 123). Fish remains are fairly common, although mostly very fragmentary. Few specimens have been found immediately associated with the insect fossils; the classic exception is the beetle *Elaterina liassica* Gardiner which was found in the eye orbit of a fish fossil during acid preparation (p. 164). Fragmentary plant remains are common, although the only close association of plants and insects is in the Woodstone where the insects appear to have been trapped by mud accumulated alongside the wood before fossilization.

The calcareous mudstone in which the insects are preserved varies in fineness and is frequently full of burrows made by organisms when the mud was still wet. The preservation varies from almost complete insects to isolated body sclerites or fragments of wings. Often very fine detail shows clearly as, for example, the fine hairs on the Orthophlebiidae (Fig. 48b). The hairs are usually not preserved as surface features but are preserved in the rock matrix and show up most clearly when the rock is wet and the surface refraction minimized. Some of the fossils show remains of cuticle, which shows up clearly when the specimen is wet. A few are preserved as impressions which show up more clearly in relief with strong lateral lighting.

The majority of the specimens are represented by single wings, and in a few cases the wings are broken, suggesting that they were subject to considerable tearing forces before fossilization. Differences in the original nature of the wings show up significantly in the deposit as differences in preservation. The toughened elytra of the beetles are more frequently preserved while their delicate and membranous hindwings are rare in the Dorset Lias. Curiously enough there are more pairs of beetle elytra preserved together than pairs of forewings of any other Order, even in the Orthoptera where the forewings are often thicker. In the Dorset rocks at least 40% of the Coleoptera are represented by paired left and right elytra, whereas in the Orthoptera both forewings are preserved in less than 8% of the specimens. The small, tough, beetle elytra were evidently less subject to dispersal than the larger Orthoptera forewings. In the Hemiptera, where the forewings of the Heteroptera are thicker, in only 12% of the fossils were the forewing and part of the body associated. In cockroaches, which have a more sclerotized forewing, only six specimens were found and each was represented by a single forewing.

There is no evidence of a concentration of insect fossils in the Flatstones and with few exceptions the fossil insects were well separated, occurring in separate blocks found scattered along some two miles of coastline. Thus although the zonal location of the blocks may be known there is no information on the *in situ* location of the fossils in the cliff face. The Jackson Collection was made over a period of many years.

The specimens were further developed (where possible) by degagement (removal of overlying rock) with a fine pneumatic hammer-drill and then studied with the surface of the rock dry, with lateral illumination from twin fibre optics, and with the surface wetted with 80% alcohol. The latter frequently enhances the appearance of the sclerotized parts and by cutting down the surface refraction permitted even fine hairs to be seen. Photographs were taken with the specimens both wet and dry. The scanning electron microscope was used to study fine details of surface features; while this was successful in some cases (Fig. 58d) it did not work where the features proved to be just below the surface. In the latter case the features could be seen when the surface was wet or by the use of episcopic illumination with ultra-violet light.

Check-list of insects from the Dorset Lias

Blattodea	*Nannoblattina petulantia* sp. nov.	114
	Rhipidoblattina sp. indet.	116
Dermaptera	*Brevicula gradus* gen. et sp. nov.	117
Odonata	*Liassophlebia pseudomagnifica* sp. nov.	120
	L. jacksoni Zeuner	121

	L. gigantea Zeuner	122
	L. anglicanopsis (Zeuner), comb. nov.	122
	Hypsothemis fraseri sp. nov.	124
	Dorsettia laeta gen. et sp. nov.	125
	Heterophlebia sp. indet.	126
Orthoptera	*Archelcana durnovaria* sp. nov.	127
	Orichalcum ornatum gen. et sp. nov.	129
	Hagla cf. *gracilis* Giebel	130
	Regiata scutra gen. et sp. nov.	131
	Protohagla langi Zeuner	133
	Protogryllus magnus Zeuner	135
	Micromacula gracilis gen. et sp. nov.	135
	Locustopsis spectabilis Zeuner	137
Phasmatodea	*Durnovaria parallela* gen. et sp. nov.	137
Hemiptera–Homoptera	*Paraprosbole rotruda* gen. et sp. nov.	141
	Tettigarctidae gen. et sp. indet.	141
	Cicadellidea, gen. et sp. indet.	141
	Mesocixiella (?) *fennahi* sp. nov.	143
Hemiptera–Heteroptera*	Gen. et sp. nov. 1A	145
	Gen. et sp. nov. 2A	145
	Gen. et sp. nov. 3A	145
	Corixidae species	146
	Mesonepa species 7A	146
	Gen. et sp. nov. 8A	146
Raphidioptera	*Metaraphidia confusa* gen. et sp. nov.	148
	Priscaenigma obtusa gen. et sp. nov.	148
Mecoptera	*Orthophlebia capillata* sp. nov.	152
	Protorthophlebia latipennis Tillyard	153
	Pseudopolycentropus prolatipennis sp. nov.	155
Diptera	*Prodocidia spectra* gen. et sp. nov.	158
Lepidoptera	*Archaeolepis mane* gen. et sp. nov.	160
Coleoptera	*Elaterina liassica* Gardiner	164
	Elaterophanes regius sp. nov.	165
	Liassocupes parvus Zeuner	167
	L. (?) *maculatus* sp. nov.	167
	L. (?) *giganteus* sp. nov.	167
	Carabidae; Byrrhoidea; Dryopoidea	169
	Curculionidae gen. et sp. indet.	169
	Coleoptera, fam. indet., spp. 1–12	170
	Holcoptera schlotheimi (Giebel)	173
	H. giebeli Handlirsch	176

Survey of the Insect Orders in the Dorset Lias

There are eleven orders of insects represented in the Jackson Collection. Orders which are known from the Jurassic or earlier, but which are not represented in the collection, are the Trichoptera, Neuroptera, Ephemeroptera and Hymenoptera. No larval stages of terrestrial or aquatic insects were found.

The best hypothesis for the derivation of the fauna is that, although the land was not far away from the marine site of fossilization (p. 183), there was no direct access to it from a freshwater site.

Blattodea. Unlike many Mesozoic faunas, cockroaches are poorly represented and only six specimens were found. Their affinities are with the many other species found in the British Purbeck and Lias formations and were representatives of widespread genera. The six specimens are placed in two species.

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* Descriptions of Mesozoic Heteroptera by Dolling, Popov & Whalley are in press.

Dermaptera. Previously the earliest earwigs known were from the Upper Jurassic of the U.S.S.R. The two specimens of a single species are the earliest representatives of the order.

Odonata. There are seven species of dragonflies in the fauna. Their affinities are in the main with species from the European Jurassic at the generic level. At the species level, most were peculiar to the Dorset fauna and indicate a different ecological origin from the rest of the British Lias. All the species are placed in extinct families and their relationship with the two extant species currently placed in the same suborder, Anisozygoptera, is not clear; they look like specialized side-branches from the main Anisozygoptera stem. *Dorsettia laeta* sp. nov. (p. 125), which shows sexual dimorphism of the wings, is the earliest example of this in the Odonata. No nymphal forms have been found.

Orthoptera. Eight species of bush-cricket and true cricket are described; some, like *Protohagla langi* Zeuner, were very large insects with a wingspan of 150 mm. Although most of the species show a generic similarity to species described from the Russian Jurassic, no doubt in part because this is the most thoroughly studied, two species, *Protogryllus magnus* Zeuner and *Locustopsis spectabilis* Zeuner, have also been found in the older Planorbis Zone of the Lower Lias of Warwickshire and Worcestershire. The family Triassomantidae (p. 129) has not previously been recorded in Britain. Judged from the number of specimens of some of the crickets, they were fairly common in the fauna from which they were derived and had structures which, in Recent species, are responsible for sound production. This suggests that sound played an important part in their communication, as in present-day crickets. The family Bintoniellidae, abundant in other Lower Lias deposits in Britain (Whalley 1982), are absent from the Dorset fauna, further strengthening the case that the ecological origin of the fauna differed from that of other British Liassic deposits.

Phasmatodea. Only a single specimen of this order was found, the first example in Britain; it is placed in the extinct family Aerophasmatidae. Recent species of the order are mainly tropical or subtropical.

Hemiptera–Homoptera. Six specimens were found but their preservation in most cases is poor. The Tettigarctid cicadas are typical of many other Mesozoic faunas where they were evidently fairly common, in contrast to the Recent fauna where only two extant species are known. The fulgoroid family Cixiidae is known from the Permian and one new species is here described from Dorset.

Hemiptera–Heteroptera. Thirty specimens were found, forming a fairly high proportion of the fauna. These specimens belong to five families, two of which will be described in a forthcoming paper (Dolling *et al.*, in press). All the landbugs belong to extinct families whereas the waterbugs can be placed in Recent families, a conclusion similar to that of Popov & Wootton (1977) in their study of the Upper Lias of Germany.

A well-preserved belostomatid waterbug (p. 146), which is broadly similar to Recent species, differs in the form of the tarsi. In Recent species these are fused to the tibia and form a unified grasping structure whereas in the Liassic fossil the tibia and tarsi are not fused and therefore a slightly different method of grasping the prey must have been used. In a number of the fossil Heteroptera, particularly conspicuous in this belostomatid, there is a reddish patch in exactly the same position as the metasternal gland of Recent species—which is also red in colour (Fig. 42, arrowed). The gland is characteristic of Recent Heteroptera and has not previously been reported in fossils. In the fossil the 'contents' of the gland are now calcitic but a preliminary analysis of the red material shows that it has a 12% sulphur content.

Raphidioptera. There are relatively few extant species of this order and there are clear indications from the fossil record that it was commoner and more diverse in the Mesozoic. Both the species described are placed in one of the extinct families.

Mecoptera. These are fairly common in the Dorset Lias and are represented by three species, all belonging to extinct families. Two are species of Orthophlebiidae which are common in Liassic deposits in Britain and elsewhere. The third species belongs to one of the more enigmatic fossil families in the Mecoptera, the Pseudopolycentropodidae, previously known only from the Upper Jurassic of continental Europe and Asia. The wings of species in this family are a very characteristic shape, differing from the widespread orthophlebiids which tend to have a more elongate, rounded wing (p. 155). The change in shape of the wing of the pseudopolycentropodids has brought about a change in the shape of the median cell and a realignment of the veins bordering this, presumably to increase the strength of the more triangular wing.

Diptera. Although two specimens are known from the Dorset Lias (p. 157), only one is clearly recognizable and it is provisionally placed in one of the Recent families of Fungus-gnats (Mycetophilidae). The Fungus-gnats of the Superfamily Bibionomorpha, to which the Jurassic specimen is assigned, are known from the Trias and Jurassic of the U.S.S.R. but are not common in the fossil record, although these delicate insects are widespread and abundant today.

Lepidoptera. The small, scale-covered, insect wing from the Dorset Lias is one of the more unexpected, and at the same time enigmatic, discoveries. There is insufficient data from the specimen to be certain of its taxonomic position within the Lepidoptera.

Coleoptera. Beetles are the most abundant and diverse of the fossils in the Dorset Lias, and while this reflects the actual diversity of beetles in the Mesozoic, it is also the result of their natural toughness and resistance to mechanical disintegration. The click-beetles (Elateridae) are the earliest known, and the preservation of the peg-mechanism on the base of the prothorax and mesothorax shows that these Jurassic forms functioned in a similar way to Recent species. The similarity of the fossil to Recent species is such that it can be placed in the Recent family Elateridae.

The Dorset cupedid beetles have elytral patterns typical of the group, which was abundant and diverse in the Mesozoic although there are few living species.

Probably the most enigmatic fossil beetles are the species of *Holcoptera*. These are common fossils in the British Lias and Upper Trias but are not known from any other part of the world. They are very distinct, with characteristic black-and-white stripes (Figs 82–87), but because little is known of parts other than the elytra it has not been possible to assign them to a Recent family. They have some general similarities to Recent *Julodis* (Buprestidae), but as yet other structural details for comparison have not been found. They are so distinctive that they may well prove to be useful as stratigraphic indicators.

Systematic section

In the following descriptions, all the specimens listed under 'Other material' are excluded from the type series. All numbers given are BM(NH) register numbers, unless otherwise stated.

Order **BLATTODEA**, cockroaches

There are still many problems in the classification of the Blattodea, because taxonomists do not agree on the major divisions of the group. Vishnyakova (1968) placed some of the Mesozoic cockroaches in the Blattidae, a family currently in use for Recent species. In the classification adopted here I do not associate the Recent and Mesozoic species in the same family but follow Fujiyama (1973), who raised the subfamily Mesoblattininae to family status. He included in the family Mesoblattinidae all the species Vishnyakova (1968) and Rohdendorf (1962) placed in the subfamily, and this classification is also followed in a study of Lower Cretaceous insects (Whalley & Jarzembowski 1985: 387). The family Blattidae is retained for geologically Recent and extant species.

Over 50 species of cockroaches, placed in 20 genera, have been described from the Jurassic rocks of Britain. Nearly half of these were considered *incertae sedis* by Handlirsch (1906), while others have been transferred to different orders (e.g. *Pterinoblattina intermixta* from Blattodea to Neuroptera). Cockroaches usually form a high percentage of fossil insect faunas (Fujiyama 1973), but in the Dorset Lias there are only six specimens out of more than 400 insect fossils.

The classification of Mesozoic cockroaches is based mainly on wing venation. Many of the wings, described as distinct species, have only very small differences of venation. In Recent cockroaches the forewing venation may vary considerably between specimens of the same species, but until the work of Vishnyakova (1964) intraspecific variation had not been considered in Mesozoic species. Vishnyakova considered that only the median vein was relatively constant and that some of the specific diagnoses previously based on venation differences were probably only intraspecific variation.

Two types of forewing were found in the Lias which are considered here as distinct species. One species has a rather narrow and heavily sclerotized forewing with a strongly curved costal margin (*Rhipidoblattina*), while the other is larger and broader. The possibility was considered that these wings represented one sexually dimorphic species. However, in sexually dimorphic Recent species the forewing of the female is usually shorter, broader and more rounded than in the male, while in the fossils the more rounded wing is much larger than the other. Since there are other differences in the venation of the anal area and in the curvature of the cubital vein, the two types of wing are regarded as distinct species. The Dorset cockroaches, which are from the Obtusum Zone, are different from cockroaches described from the older Planorbis Zone from the west Midlands.

Family **MESOBLATTINIDAE** Handlirsch, 1906

Subfamily **MESOBLATTININAE** Handlirsch, 1906

The subcostal area of the forewing is small and the subcostal vein cannot usually be distinguished. Upper Carboniferous – Upper Jurassic. Cosmopolitan.

Genus *NANNOBLATTINA* Scudder, 1886

[Scudder 1886: 475, 1890: 376; Handlirsch 1906: 533]

TYPE SPECIES. *Nannoblattina prestwichi* Scudder 1886: 475, here designated. Jurassic, Europe.

DIAGNOSIS. R and M fused for part of their length in the forewing.

REMARKS. Although there are several species of *Blattula* Handlirsch in which R and M are joined (Vishnyakova 1968), in other Mesozoic cockroaches these veins are separate. Species of *Blattula* where R and M are joined are much smaller than *Nannoblattina*. No type-species designation has hitherto been made for this genus, which has three included species: I have selected as type the species with the most complete type specimen.

Nannoblattina petulantia sp. nov.

Fig. 1a, b

DIAGNOSIS. As genus; anal veins angled.

NAME. 'Capriciousness'.

DESCRIPTION. Forewings, subcostal vein unbranched, subcostal area small. R with parallel branches, some basal and apical ones forked, running to costal margin. Intercalary veins present. M with two main branches off MA, with at least two further branches off each of these. Base of M obscured, possibly joining R near centre of wing but may run contiguously all along R to base. Cu strongly curved, clearly separate from base of R + M, branches from Cu curved forward. Anal area reticulate, some of the veins branched near the margin.

HOLOTYPE. In.53929; Flatstones, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: length 16·3 mm; width 8·3 mm; anal area 9·4 × 4·5 mm.

OTHER MATERIAL. In.51004.

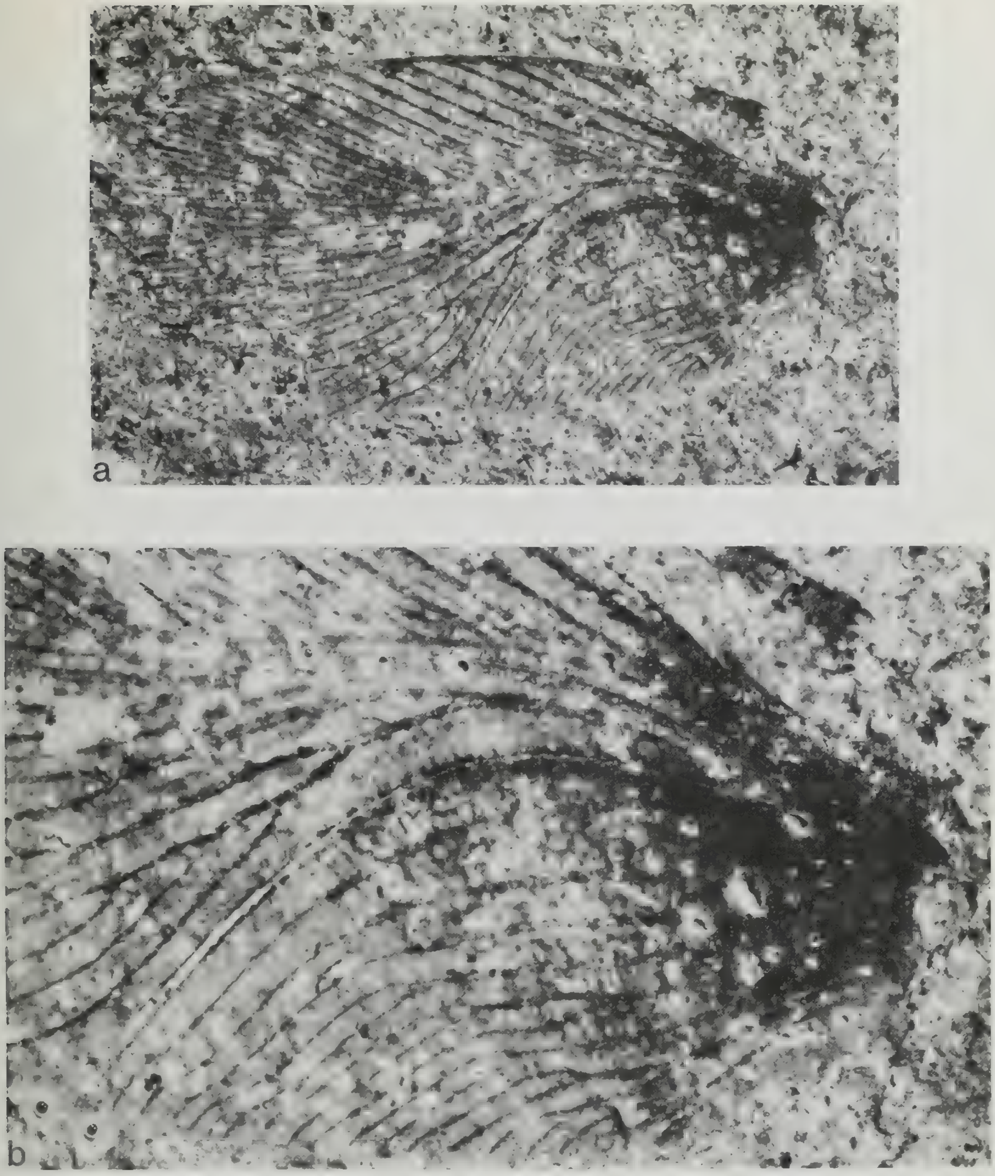


Fig. 1 *Nannoblattina petulantia* sp. nov. (Blattodea). **Holotype**, In.53929. a, forewing, 16·3 mm long. b, forewing, venation of anal area.

Discussion. The second specimen In.51004, although basically similar to the holotype, has a narrower anal area and the cubital vein, while curved, does not dip down as sharply as in the holotype. There is, in the holotype specimen, a trace of a vein close to the radius which might be the base of the medial vein, but even just anterior to the centre of the wing it appears to fuse with the radius. The shape of the anal area, the arrangements of these veins and the curved posterior branches of the cubital are characteristic of this species. It is much larger than the other species of *Nannoblattina* previously described from the British Lias or Purbeck beds.

Genus ***RHIPIDOBLATTINA*** Handlirsch, 1906
Fig. 2

TYPE SPECIES. *Mesoblattina geikiei* Scudder, 1890, by monotypy.

The remaining four specimens of Mesoblattininae from the Dorset Lias are incomplete and cannot be more closely identified. They are all basically similar and have slender forewings with a strongly curved costal margin that is heavily sclerotized, and a rather truncated anal area. The radial vein is gently curved but the details of the rest of the wing are not preserved. On the evidence available they are only provisionally placed in *Rhipidoblattina* (Handlirsch 1906: 531).

MATERIAL EXAMINED. In.49212; In.49249; In.53909; In.53920 (Fig. 2).

DIMENSIONS. 14 mm (estimated complete wing length, under 15 mm).

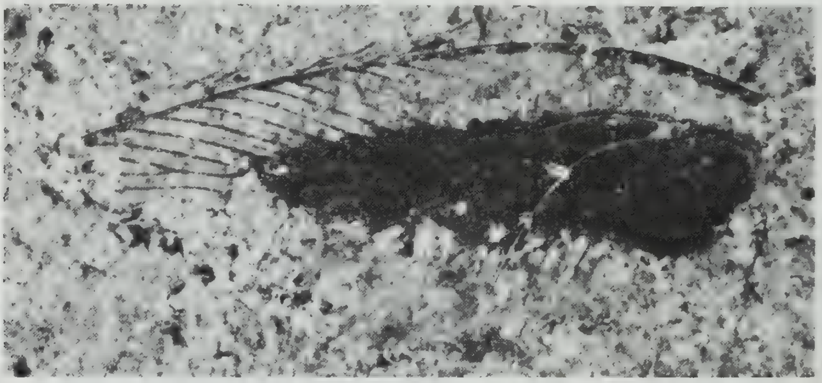


Fig. 2 *Rhipidoblattina* sp. (Blattodea). In.53920, forewing, 14 mm long.

Order **DERMAPTERA**, earwigs

The earliest earwigs previously known are from the Upper Jurassic of the U.S.S.R. The two specimens from Dorset differ from Recent Dermaptera mainly in the ornamentation of the tegmina, which in most Recent species is smooth. No veins could be seen in the forewing (tegmina), which is shorter than the abdomen, although there may have been a trace of a subcostal vein.

Suborder **ARCHIDERMAPTERA**

DIAGNOSIS. Tegmina reaching well down abdomen. Tarsi 4–5 segmented.

REMARKS. Only one family and genus, from the Upper Jurassic of Kazakhstan, are currently known in this suborder.

Family **PROTODIPLATIDAE** Martynov, 1925*b*

DIAGNOSIS. As suborder.

The new genus described below is provisionally placed in this family. Western Europe, Jurassic.

Genus ***BREVICULA*** nov.

TYPE SPECIES. *Brevicula gradus* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Tegmina strongly punctate, reaching at least to second abdominal segment. Coxae short, rounded.

NAME. 'A little thing'.

Brevicula gradus sp. nov.

Figs 3–4

Diagnosis. As genus.

Name. 'A step'.

Description. Head prognathous; antennae incomplete, multisegmented. Possible Y-shaped suture on head. Thorax rounded. Tegmina strongly punctate, probably reaching third abdominal segment, rather slender (and possibly pointed but incomplete apically). Hindwings indistinct. Abdomen parallel-sided but terminal segment rounded. Terminal process possibly at least two-segmented, elongate. Legs cursorial, slender. Femora slightly thickened; 4–5 segmented tarsi.

Holotype. In.53993 (Fig. 3); Flatstones, Black Ven, Charmouth, Dorset. Jackson colln. Dimensions: Body 10 mm (including cerci); cerci 1·5–2 mm. Tegmina 4·4 mm.

Paratype. In.51036 (Fig. 4); data as holotype.

Discussion. The strongly punctate tegmina conceal most of the folded wings in the fossil. Consideration was given to the possibility that the specimens represented a nymphal orthopteran or a brachypterous adult orthopteran, but the lateral displacement of the tegmina, which appear to be devoid of veins, would be unusual in these, but would not be unexpected in a fossilized dermapteran. It is not possible to count the exact number of tarsal segments, of which there are certainly four and may well be five. The apical cerci are difficult to interpret. In one specimen there is an indication that they may be segmented, perhaps with two segments, but in the other there is a longitudinal separation into two rather slender, and apparently lightly sclerotized, processes (forceps). The only coxa showing is on the foreleg where it is clearly short and rounded; this condition is regarded as more primitive than the long conical coxae of the Blattopteroidea. However, Hennig (1981) took the opposite view and said that the short coxae of the Dermaptera could have been a derived character.

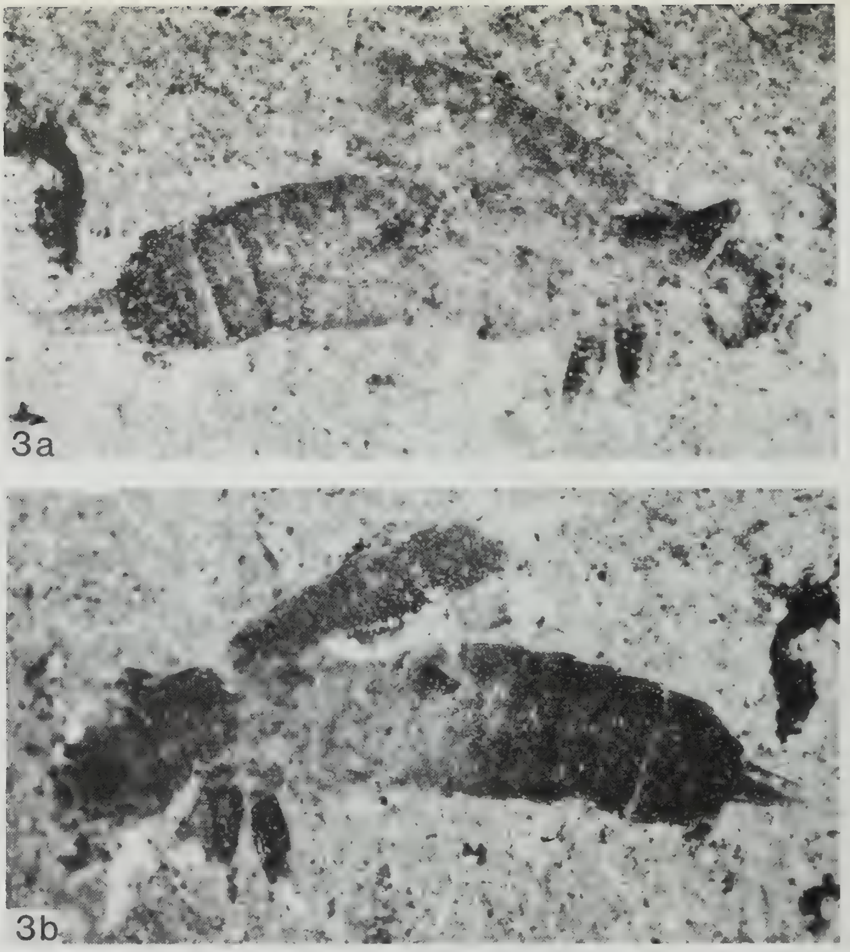
Order **ODONATA**, dragonflies

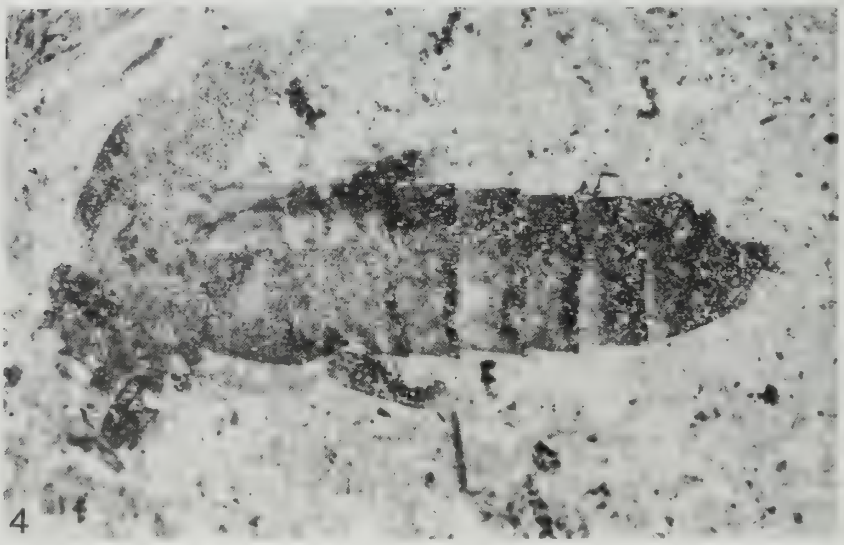
There is still some dispute over the major classification of this order. Much of our information is based on the work of Tillyard & Fraser (1938–40) and of Fraser (1957) although Carle (1982) reviews some aspects of their phylogeny. A recent interpretation of the classification within the order by Pritykina (1980) differs considerably from the earlier work. The traditional classification (Tillyard & Fraser 1938–40, Cowley 1942, Fraser 1957 and most textbooks) uses three main suborders in the Odonata, the Anisoptera, Zygoptera and Anisozygoptera, although Fraser (1957) listed four more suborders for fossil species (Protozygoptera, Archizygoptera, Meganisoptera and Protoanisoptera). The Anisoptera and Zygoptera are widely used in the literature although the latter is sometimes regarded as paraphyletic (Hennig 1981). It is, however, within the Anisozygoptera that there has been most controversy. An outline definition of the three suborders used here and based on Fraser (1957) is given below.

In the Anisoptera, in both fore and hind wings, a cross-vein divides the discoidal cell into an anterior and a posterior triangle. Both these triangles may be further subdivided by cross-veins.

The Zygoptera have the same shaped fore and hind wings, generally with a narrow base to the wing. The wings have either an open or a closed discoidal cell below the arculus. In some genera (e.g. *Hemiphlebia* Selys) the discoidal cell may be open in the forewing and closed in the hindwing; more frequently both wings have a closed discoidal cell. Within the Zygoptera further subdivisions are made based on the shape of the discoidal cell and the number of antenodal veins.

The Anisozygoptera of Handlirsch are known mostly as fossils from the Mesozoic and there are only two living species of *Epiophlebia* Calvert that are placed in this suborder; this is the





Figs 3–4 *Brevicula gradus* gen. et sp. nov. (Dermaptera). Fig. 3, **holotype**, In.53993. a, part, 10 mm long. b, counterpart. Fig. 4, paratype, In.51036.

traditional concept. But Imms (1970: 307) stated 'it is not easy to frame a definition of this suborder (i.e. Anisozygoptera) to embrace its many Mesozoic forms'. In the Recent species the base of the wing is narrow while it is broad in the fossils. The discoidal cell is normally square in the hindwing but may be a different shape in the forewing. Asahina (1954) divided the Anisozygoptera into two superfamilies, placing the two living species of *Epiophlebia* in the Superfamily Epiophleboidea, separating them from the fossil species which he placed in the Heterophleboidea. He stated that the Epiophleboidea are 'most closely related to the Heterophleboidea of the Lias period' and then added 'if considered from venational characters there seems to be enough reason to include both groups within the same suborder' (i.e. Anisozygoptera).

Pritykina (1980) emphasized, however, the differences between the fossil and Recent 'Anisozygoptera' in her classificatory diagram (1980: fig. 611). She also used a different nomenclature for the various groups; her names are given in brackets in the following account. Her diagram can be interpreted as showing a sister-group relationship between the Anisoptera (Libellulomorpha) and Recent Anisozygoptera (Epiophleboidea). She had an enlarged group called Lestomorpha in which she placed the Zygoptera and all the Mesozoic 'Anisozygoptera'. She clearly regarded the Mesozoic anisozygopteran genera as being more closely related to the Zygoptera than to the Anisoptera or Recent Anisozygoptera.

Zygoptera first appear in the fossil Record in the Permian (*Permagrion* Tillyard). There is still some dispute over the earliest Anisopteran but there is no doubt they were much later than the Zygoptera. *Liassogomphus* Cowley from the Upper Lias in Gloucestershire was accepted as a true anisopteran by Tillyard (1925) and Cowley (1942), although Fraser (1957) places it in the Anisozygoptera. There is a typical anisopteran triangle in *Liassogomphus* and Pritykina (1968) described several Jurassic Anisoptera. Hennig (1981) placed *Liassogomphus* as possibly the stem-group of the Anisoptera and Anisozygoptera. In the present study the Mesozoic fossils are placed provisionally in the Anisozygoptera pending a further analysis of the major classification of the Odonata.

If the fossil and Recent Anisozygoptera (as traditionally interpreted) form a monophyletic group, it is obvious that it was far more abundant in the Mesozoic than it now is, having only two living species. Comparing all the present-day Odonata with their fossil record and considering the species diversity, one may conclude that Odonata were possibly more abundant in the Mesozoic than at the present day; it is interesting to speculate on factors which might have allowed this. The most obvious one is the almost complete lack of birds as predators in the early Mesozoic. No doubt insects, including dragonflies, were the prey of some of the Mesozoic pterosaurs, but it was the appearance of insect-eating birds later in the geological record that provided the first real competition for the predatory aerial dragonflies. Probably it was competition for the aerial insects as food as much as direct predation on the dragonflies themselves which materially affected their abundance. Thus while dragonfly-like forms had been the only or the main aerial predators of flying insects since the Upper Carboniferous, their zenith was passed in the Mesozoic and the present-day species are the remnants of a much larger Mesozoic fauna. Even the size has decreased, from the giant dragonfly-like predators of the Palaeozoic with wingspans of 600 mm, to the present-day forms, the largest of which is well under 200 mm. Many of the Mesozoic species had a larger wingspan than any of the living species. While the birds may have been one of the factors in the faunal decline of the Odonata, there were probably others that have not yet been identified.

Suborder **ANISOZYGOPTERA**

Family **LIASSOPHLEBIIDAE** Tillyard, 1925

DIAGNOSIS. Fore- and hindwings differ in venation. Discoidal cell often open posteriorly in forewing. Usually only two antenodal cross-veins.

Western Europe, Jurassic.

Genus ***LIASSOPHLEBIA*** Tillyard, 1925

TYPE SPECIES. *L. magnifica* Tillyard 1925: 13, by original designation.

DIAGNOSIS. Only two antenodals. Discoidal cell irregular, not square or rectangular.

Jurassic, Europe.

Liassophlebia pseudomagnifica sp. nov.

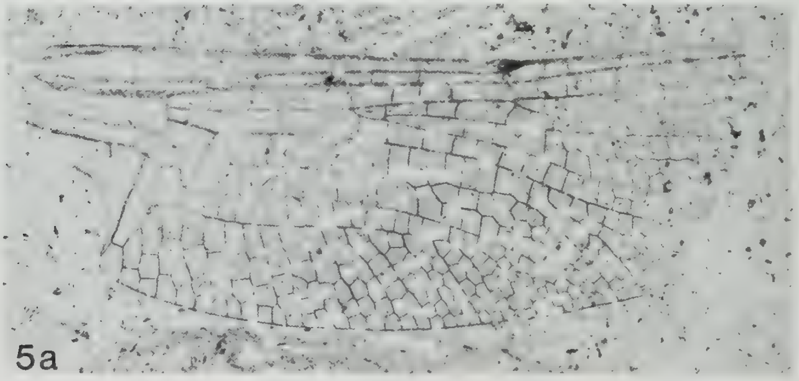
Fig. 5a, b

1962 *Liassophlebia magnifica* Tillyard; Zeuner: 162; pl. 27, fig. 1.

DIAGNOSIS. *Liassophlebia* with double row of polygonal cells in area between M and Cu.

NAME. Not true *magnifica*.

DESCRIPTION. Single hindwing; apical half missing. Venation as in Fig. 5a. Costal vein thick at base; two antenodals, 7 mm apart. Arculus strongly recurved. Discoidal cell closed. Node approximately 25 mm from wing base.



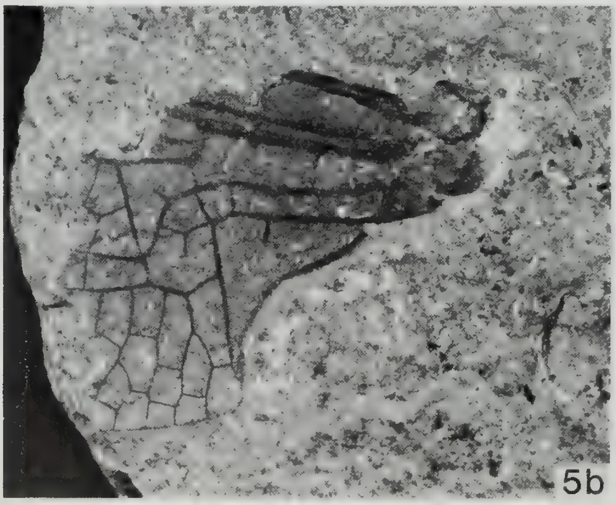


Fig. 5 *Liassophlebia pseudomagnifica* sp. nov. (Odonata). **Holotype**, In.64000. a, part, hindwing, 39 mm long. b, counterpart, wing base.

HOLOTYPE. In.64000; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: length (incomplete) 39 mm, estimated wing length 50–52 mm.

DISCUSSION. The holotype has been prepared by degagement, i.e. uncovering more of the fossil by removal of overlying rock. This has revealed more details than were available to Zeuner (1962), who identified this specimen as *L. magnifica* Tillyard. Comparison of the newly-revealed basal part of the wing with the type of *L. magnifica* shows that, apart from some differences in cell shapes, *L. pseudomagnifica* is also substantially smaller. In *L. magnifica* the node, at 35·4 mm from the base, is almost equidistant from the tip of the wing. In the incomplete wing of *L. pseudomagnifica*, on the other hand, the node is 25 mm from the base of the wing: if the two wings had similar proportions, this would mean a total wing length of 50 mm for *L. pseudomagnifica*. The wingspan of *L. magnifica* was about 140 mm, whereas that of *L. pseudomagnifica* was only 100 mm.

The possibility that *L. pseudomagnifica* was the (smaller) male of *L. magnifica* was considered. Variation in wing length in the Recent Anisozygoptera was discussed by Asahina (1954), who showed that a maximum variation within one species was 4 mm in the male and 3 mm in the female, well below the difference between *L. magnifica* and *pseudomagnifica*; they are clearly not individual variants of one species. The number of cells in the cubital and anal areas, the shape of the discoidal cell and the reduction in number of antenodals separate *L. pseudomagnifica* from Recent species of *Epiophlebia*, while the fossil species, *L. jacksoni*, is much smaller.

Specimen In.49213 was also incorrectly identified as *L. magnifica* by Zeuner (1962: 162); it may well be *pseudomagnifica* but no further development has been possible.

Liassophlebia jacksoni Zeuner, 1962

Fig. 6

1962 *Liassophlebia jacksoni* Zeuner: 162; pl. 25, figs 1, 2.

Only a small amount of development of the specimen has been possible since Zeuner examined it and this does not materially alter his interpretation of the species. A further 8 mm of wing has been exposed, giving a preserved length of 75 mm. Zeuner's estimate of wing length of 83 mm is reasonable.

HOLOTYPE. In.53999; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln.

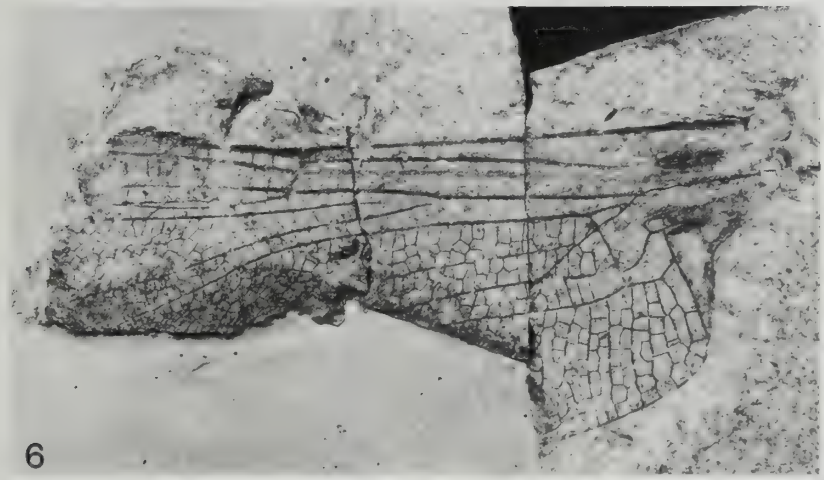


Fig. 6 *Liassophlebia jacksoni* Zeuner (Odonata). Holotype, In.53999. Hindwing, 75 mm long.

Liassophlebia gigantea Zeuner, 1962

Fig. 7a, b

1962 *Liassophlebia gigantea* Zeuner: 163; pl. 27, fig. 2.

This forewing has been developed further since it was examined by Zeuner but the newly-revealed parts do not alter his interpretation. The full shape of the discoidal cell is revealed as elongate and lying almost at right angles to the main axis. The discoidal cell is closed at the posterior margin, unlike *L. magnifica* where the cell is open in the forewing, although closed in the hindwing. The development of the wing has exposed the nodal area and also clearly shows the strongly curved base of the costa.

HOLOTYPE. In.51030; Woodstones, Black Ven, Charmouth, Dorset. Jackson colln.

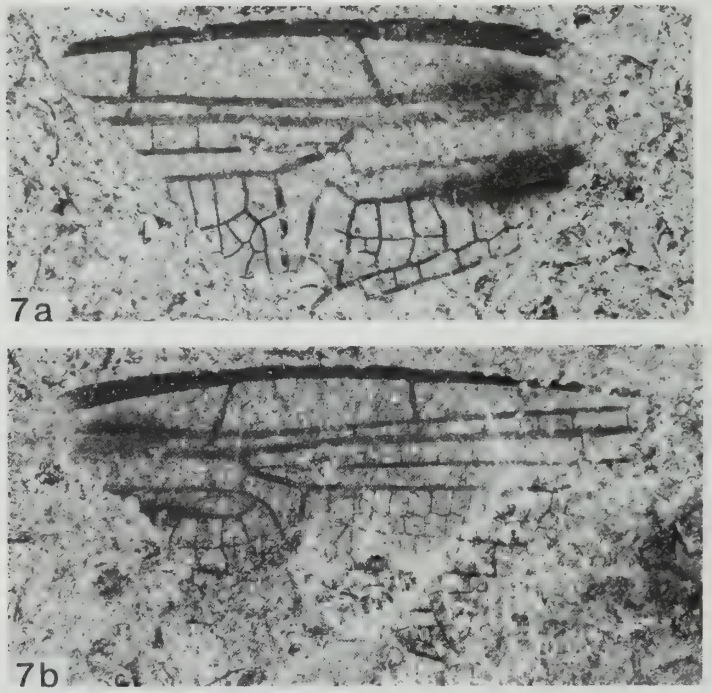


Fig. 7 *Liassophlebia gigantea* Zeuner (Odonata). Holotype, In.51030. a, part, wing length *c.* 33 mm (incomplete). b, counterpart, wing length *c.* 24 mm (incomplete).

Liassophlebia anglicanopsis (Zeuner) 1962, comb. nov.

Fig. 8a, b

1962 *Petrophlebia anglicanopsis* Zeuner: 160; pl. 24, figs 1, 2.

By degagement it has been possible to develop this specimen, revealing far more than could be seen when Zeuner examined it. The incomplete wing seen by Zeuner was only 34·5 × 15 mm, but using the fine pneumatic drill to remove the overlay, 64 × 20 mm of it has now been revealed. In spite of this, Zeuner's original estimate of the total wing length (80 mm) is still considered reasonable. He commented that 'the poor condition of the wing, with its corroded edge, suggests prolonged drifting' (Zeuner 1962: 161), but this is untenable in the light of the new evidence revealed by development. The wing was not in poor condition but the 'corroded' edges were buried immediately below an ammonite (*Asteroceras obtusum* J. Sowerby): when the

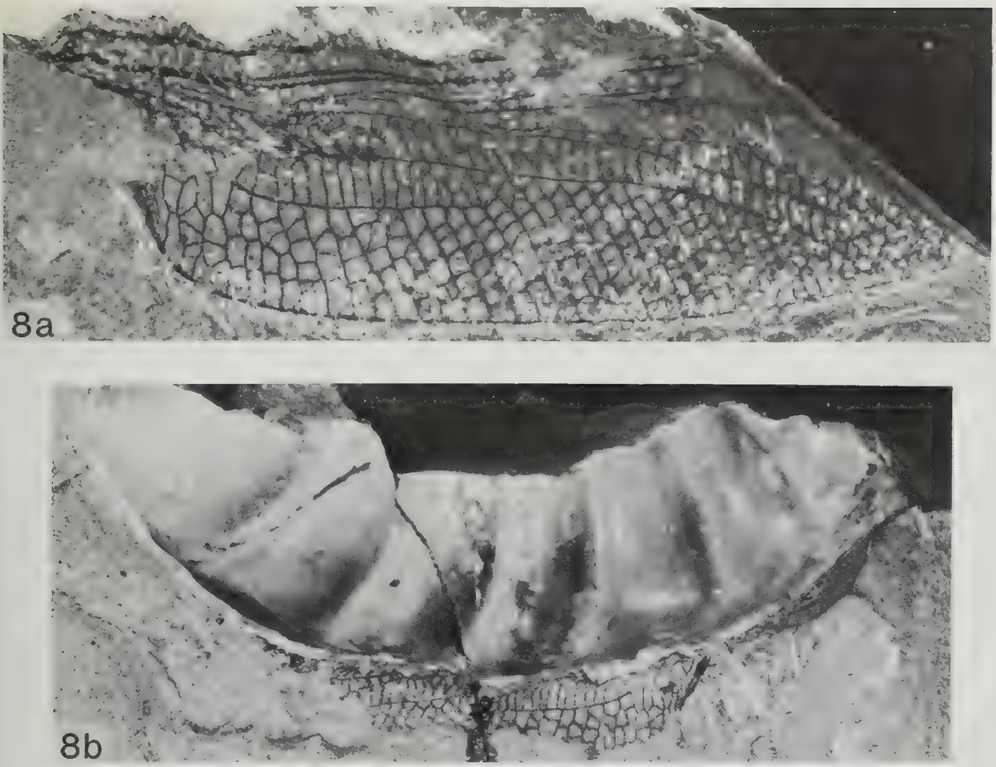


Fig. 8 *Liassophlebia anglicanopsis* (Zeuner) (Odonata). Holotype, In.49573. a, part, hindwing 64 mm long. The white patches near the anterior margin are the remains of an ammonite: this was overlying the wing and caused the slight deformation, visible as slightly wavy lines along the anterior margin. b, counterpart, ammonite not removed.

ammonite shell was removed the wing was found to have been deformed by its weight pressing on it while the Jurassic mud was wet, but the wing had not been torn. The wavy shape of the wing reflects the shape of the ammonite pressed into it. It appears the wing had stuck on the mud and the ammonite had come to rest on it, deforming it slightly. The alternative hypothesis, that the wing had washed up against a partly buried ammonite shell, does not seem tenable from a study of the specimens. There was no sediment between the wing and the ammonite shell, suggesting that their burial was simultaneous.

The further development of the wing has revealed most of the basal area, together with the discoidal cell; this has shown that the generic position assigned by Zeuner was incorrect. No further development of the second specimen (In.59376) mentioned by Zeuner has been possible and it may or may not be conspecific with *L. anglicanopsis.*

HOLOTYPE. In.49573; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln.

Genus ***HYPSOTHEMIS*** Pritykina, 1968

TYPE SPECIES. *Hypsothemis jurassica* Pritykina 1968: 41, by original designation.

DIAGNOSIS. Both distal angles of quadrangle (discoidal cell) acute. Posterior margin (of cell) slightly longer than anterior side. Posterior margin of wing without strong anal angle. Anal vein turns towards margin of wing level with centre of quadrangle (Pritykina 1968, in part).

Jurassic, Asia.

Hypsothemis fraseri sp. nov.
Fig. 9

1962 *Liassophlebia magnifica* Tillyard; Zeuner: 162 (part).

DIAGNOSIS. Discoidal cell with broader apical side. Single row of veins form large cells in between M and Cu.

NAME. After the late F. C. Fraser, a specialist on Odonata.

DESCRIPTION. Incomplete hindwing with two antenodals. Discoidal cell with very long distal side and row of slightly sinuous veins between M and Cu. Large cell below discoidal between CuA and CuP at angle to long axis of wing; the cell may be divided but this is not clear in the specimen. Anal cells in regular arrangement along basal margin. Some anterior basal sclerites preserved with long fine hairs attached.

HOLOTYPE. In.59106; Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: 40 × 16 mm (incomplete). Distance between antenodals, 5·5 mm.

OTHER MATERIAL. In.59109; data as holotype.

DISCUSSION. Degagement of this wing has allowed a study to be made of many more veins than were available to Zeuner (1962), who incorrectly identified it as *L. magnifica* Tillyard. In particular all the cells in the basal area of the wing have been exposed. The holotype is broadly similar to *Hypsothemis jurassica* Pritykina, but differs in having three rows of cells in the anal and four in the postcubital areas, whereas *H. jurassica* has only two in the anal and three in the postcubital area and is a smaller species. The genus *Hypsothemis* was previously known only from the type species from Asia. The Dorset specimen has part of the hairy base of the wing preserved near the costal margin. The exact shape of the cell (quadrangular) immediately below the discoidal cell is not entirely clear in the fossil but is probably longer than wide.

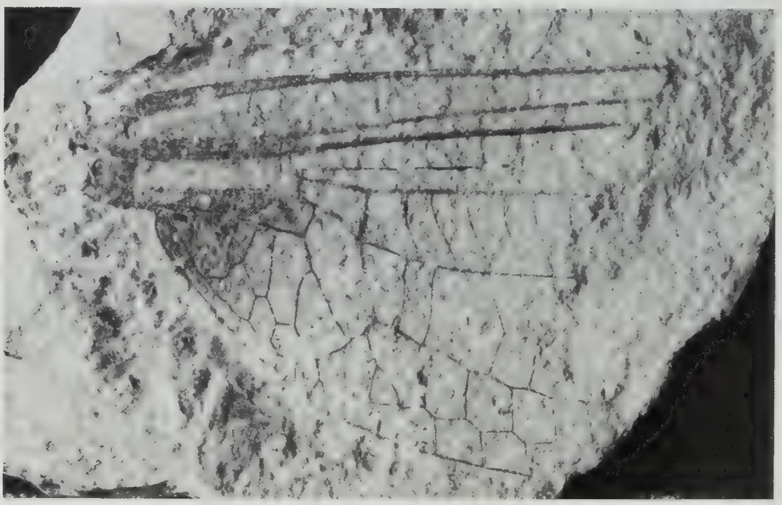


Fig. 9 *Hypsothemis fraseri* sp. nov. (Odonata). **Holotype**, In.59106, hindwing, 40 mm long.

Family **ARCHITHEMISTIDAE** Handlirsch, emend. Cowley, 1942

Genus ***DORSETTIA*** nov.

TYPE SPECIES. *Dorsettia laeta* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Discoidal cell elongate, almost rectangular. Cross-veins between M and Cu, CuA and CuP almost parallel, forming row of elongate cells between each pair of veins.

NAME. From the county of Dorset.

The genus is very distinct from other Mesozoic genera and its relationship is not clear. Provisionally it is placed near *Diastatommites* Handlirsch, but differs in the large single cells in the area between the cubital veins.

Dorsettia laeta sp. nov.
Fig. 10a, b

1962 ? *Diastatommites liassina* (Strickland); Zeuner: 164; pl. 27, fig. 3.

DIAGNOSIS. As genus.

NAME. 'Joyful'.

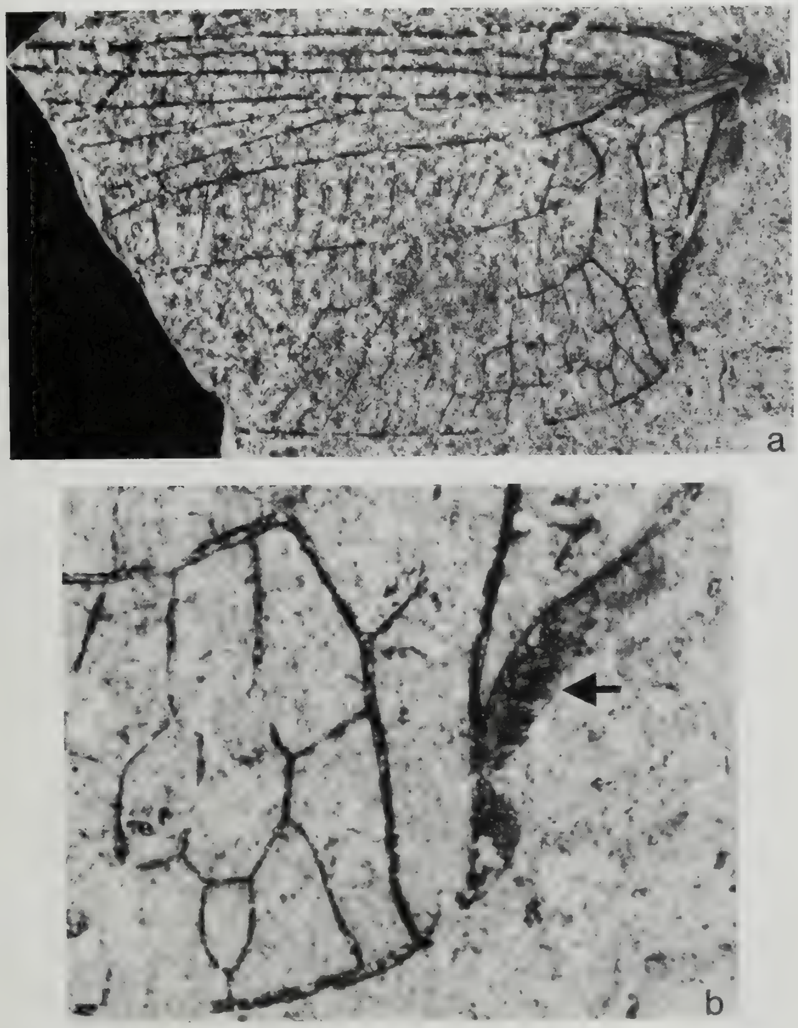


Fig. 10 *Dorsettia laeta* gen. et sp. nov. (Odonata). **Holotype**, In.59375. a, hindwing, 37 mm long. b, base of same wing to show hairs (arrowed).

DESCRIPTION. Incomplete male hindwing. Probably only two antenodals. Node 30 mm from base of wing. Setal bases along veins in discoidal and cubital rows. Sub-discoidal cell elongate. Anal cells elongate, almost at right angles to long axis of wing. Basal hind margin sclerotized and hairy.

HOLOTYPE. In.59375; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 37 mm (incomplete) × 13·5 mm. Estimated total wing length 60–65 mm.

DISCUSSION. Very little of this specimen was seen by Zeuner, who provisionally identified it as a species of *Diastatommites* (Zeuner 1962: 164). Degagement has cleared all the overlying rock. The wing node, 30 mm from the base of a wing 13–14 mm wide, suggests a very broad, though relatively short, wing. The discoidal cell of *Dorsettia* is similar in shape to many Mesozoic Anisozygoptera.

The specialization of the basal part of the wing is similar to many Recent Corduliinae (Anisoptera): this type of broad, modified base is found in males where sexual dimorphism in wing shape occurs. Hence the specimen of *Dorsettia* is considered to be a male; in this species there was probably sexual dimorphism, in which case the female wing would show simpler structure. Perhaps we have here the earliest example of such sexual dimorphism in the Odonata.

Family **HETEROPHLEBIIDAE** Handlirsch, 1906

Genus ***HETEROPHLEBIA*** Westwood, 1849

TYPE SPECIES. *Agrion buckmanni* Brodie 1845, by monotypy (Westwood 1849: 32). Upper Lias, U.K.

The single incomplete specimen from Dorset lacks the costal margin and much of the anterior part of the wing. There is also a fault in the rock in the area of the triangle. The cubital veins curve backwards strongly but the preservation is such that this specimen is only provisionally placed in *Heterophlebia*.

MATERIAL. In.49246; Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Length 15 mm, estimated wing length 30–40 mm. Distance between antenodals, 5·5 mm.

Odonata indet.

In.53895 and In.53972, mentioned by Zeuner (1962: 164), are possibly parts of *Liassophlebia* wings.

Order **ORTHOPTERA**, grasshoppers and crickets

The Dorset Lower Lias is very rich in orthopterous fossils, which make up 14% of the insect species. The fauna includes some of the largest Jurassic insects, like *Protohagla langi* Zeuner which had a wingspan of nearly 150 mm. Some of the fossils are almost complete specimens while others are represented by wings or legs only. There are also a number of isolated, unassociated insect legs, many of which are clearly orthopterous, and several of the saltatorial types were found (Figs 30–32). But it has not been possible to associate these isolated legs with particular species, although some were found not far removed from bodies of orthopterous insects. This implies that the legs, which in the Orthoptera are easily broken off the dead insect, can only have been separated from one another at a short distance from the final deposition site, particularly as a few specimens still have the legs attached. The area from which the Dorset fossils were derived was clearly rich in highly diversified Orthoptera.

The classification used in the following section is based on Sharov, 1968 (English translation, 1971).

Suborder **ENSIFERA**

Superfamily **OEDISCHIIDEA**

Fossils of the nine families in the Oedischiidea of Sharov have been found from the Upper Carboniferous to the Lower Cretaceous (Sharov 1968). The forewings are long and rather narrow in proportion to the length and lack any stridulatory organs.

Family **ELCANIDAE** Handlirsch, 1906

Genus ***ARCHELCANA*** Sharov, 1968

Type species. *Elcana britannica* Handlirsch, by original designation of Sharov (1968: 35).

Diagnosis. Elcanids with Sc simple; C with short branches and a three-branched cubital vein. More anal veins than species of *Elcana* (Sharov 1968).

Lower Lias, western Europe.

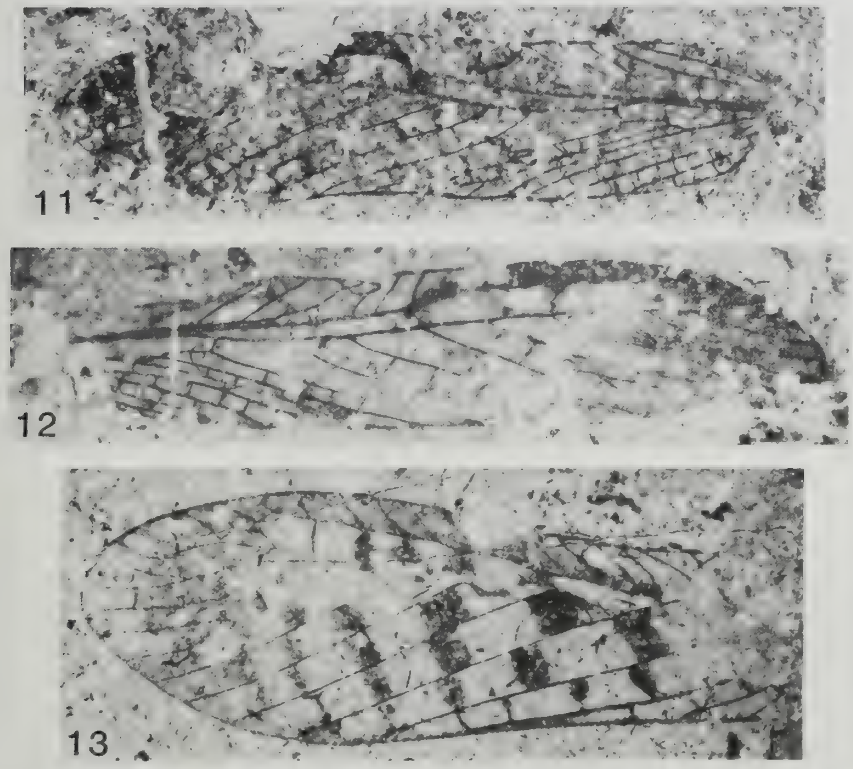
Archelcana durnovaria sp. nov.

Figs 11–15

Diagnosis. As genus, but with prominent cross-vein from M–Cu near base.

Name. Latin name of Dorchester.

Description. Forewing, costal vein short with lateral veinlets; subcostal unbranched. R_1 arises before division of MA and MP. Rs long, running forward with anterior branches to margin.



Figs 11–13 *Archelcana durnovaria* sp. nov. (Orthoptera). Fig. 11, **holotype**, In.59162, forewing, 20 mm long. Fig. 12, paratype, In.59377, forewing. Fig. 13, paratype, In.53922, forewing.

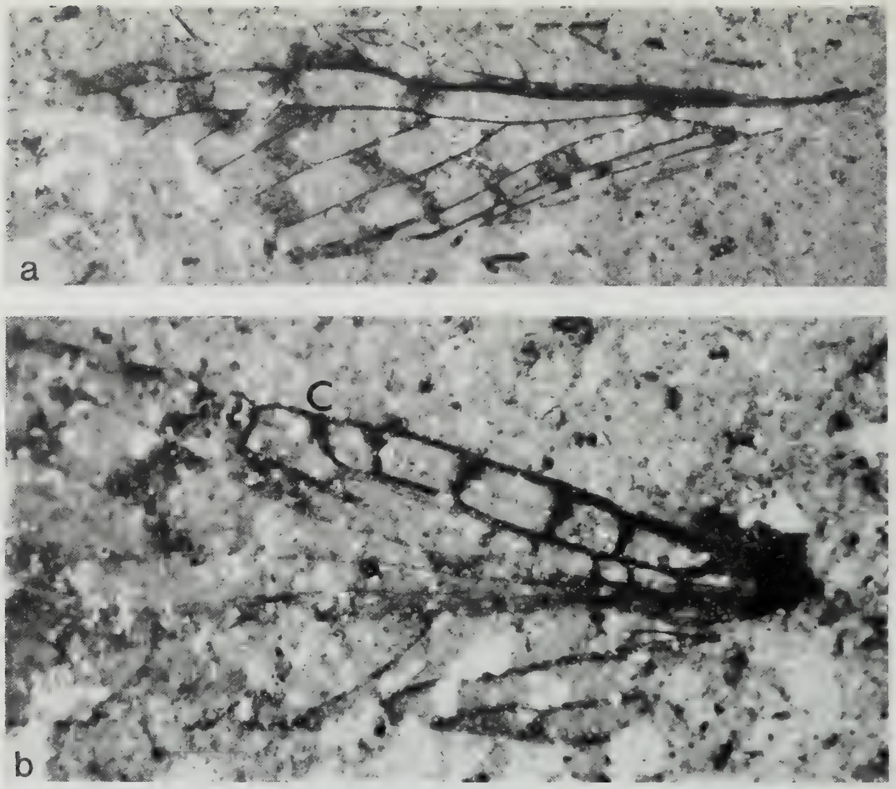


Fig. 14 *Archelcana durnovaria* sp. nov. (Orthoptera). Paratype, In.59381, forewing. a, part. b, counterpart. C = cells in anal area of wing (see p. 129).

Medial vein curves from broad stem of R + M and divides into MA and MP. Several parallel branches arise from MA. Prominent cross-vein from M to Cu where CuA curves forward. Posterior cross-vein from junction with CuA$_2$ to R + M. CuP straight with CuA$_1$ and CuA$_2$ curved forward off it. Three anal veins with cross-veins. Long (9·2 mm), curved ovipositor; segmented antennae (incomplete); eyes and antennal base preserved.

Holotype. In.59162 (Fig. 11); Woodstone, Black Ven, Charmouth, Dorset; Jackson colln. Dimensions: Wing length 20·1 mm, width 4·4 mm.

Paratypes. In.51029, In.53894, In.53922 (Fig. 13), In.59377 (Fig. 12), In.59381 (Fig. 14), In.64005, In.64038.

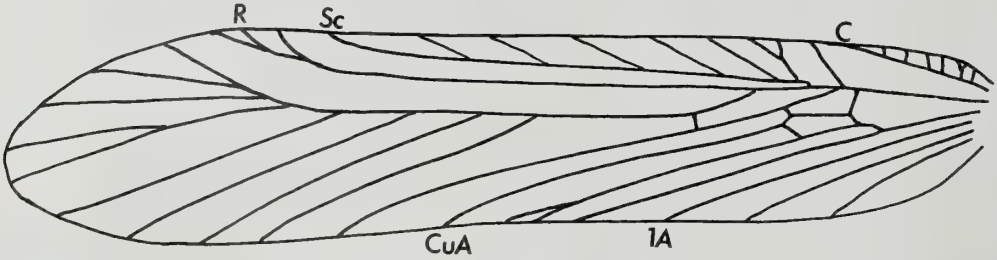


Fig. 15 *Archelcana durnovaria* sp. nov. (Orthoptera). Diagram of wing venation. 1A = first anal vein, C = costal vein, CuA = cubital veins, R = radial veins, Sc = subcostal vein.

OTHER MATERIAL. In.49203, In.49580, In.49600, In.49614, In.53900, In.53906, In.53956, In.53976, In.59139, In.59151, In.59358A, In.64001, In.64006, In.64028.

DISCUSSION. The genus *Elcana* can be separated from *Archelcana* by the number of cubital veins, two in the former, three in the latter. The type of *Elcana*, *E. tessellata* Westwood from the Purbeck beds, has only two cubital veins and has a few branches toward the anterior margin from Sc; these are absent in *Archelcana*.

Including the new species, there are three species of *Archelcana*. *A. shurabica* Sharov, from the Lower Jurassic of Asia, has additional branches on the end of the first anal vein and the subcostal vein reaches further towards the apex than in *A. durnovaria*. *A. britannica* (Handlirsch) is from the Lower Lias of Warwickshire and most closely resembles the new species: it can be distinguished by the relatively long cross-vein Mu–Cu and the shape of the base of CuA_1 and CuA_2.

Sharov (1968) considered that there was a precostal vein in this genus. This can be seen in Fig. 14b at the bottom right as an inverted Y-shaped vein. This specimen shows strongly sclerotized anal cross-veins (Fig. 14b, 'C'). This suggests that there may well have been a more heavily sclerotized forewing, probably similar to many Recent Orthoptera. The veins on the part and counterpart have separated unequally, making the two halves look rather different.

A special feature of *Archelcana* is the development of three cubital veins although the anterior one could be considered as CuA + MP. The antennal segments preserved in one specimen (In.64028) indicate that there was a long filiform antenna. The ovipositor preserved on the same specimen is slightly curved, finely pointed and evidently strongly sclerotized. Traces of the rest of the body of In.64028 are indistinct but one of the anal cerci is preserved.

Although probably all the specimens included amongst 'Other Material' are *A. durnovaria* some of the diagnostic characters are indistinct and these specimens are therefore excluded from the series of paratypes.

Family **TRIASSOMANTIDAE** Tillyard, 1922

This family was originally associated with the Mantidae by Tillyard (1922). Sharov (1968) redefined it on the basis of the short and narrow precostal area and the anterior median vein forking level with, or apically to, the origin of the radial sector vein. At present this family is known from the Triassic of Australia and Siberia.

Genus ***ORICHALCUM*** nov.

TYPE SPECIES. *Orichalcum ornatum* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Triassomantids with slender wings and an anastamosis between Rs and MA; branched costal vein which reaches the anterior margin slightly anterior of level of fork of CuA and CuP.

NAME. 'Brass'.

Orichalcum ornatum sp. nov.

Figs 16, 21

DIAGNOSIS. As genus.

NAME. 'Equipped'.

DESCRIPTION. Costal vein with short side-branches; subcostal vein extends well along front margin of wing towards apex, running closely parallel with R for much of its length. Rs branches well anterior to apex of costal vein, slightly anterior to fork of CuA and CuP. Rs short, joins MA which then has four more branches to wing margin. Three or four post-medial branches. Cu relatively simple, broadly forking well before middle of wing with forked CuA and simple CuP. Anal area long, ending just in front of origin of Rs. Anal veins close together. Strongly reticulated cells over apical portion of wing, cross-veins numerous in basal part. Some strongly pigmented areas visible, probably representing original pattern.

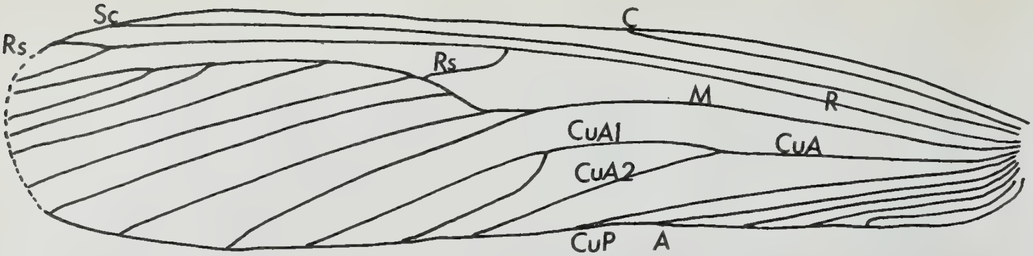


Fig. 16 *Orichalcum ornatum* gen. et sp. nov. (Orthoptera). Diagram of forewing venation. C = costal vein, CuA = anterior cubital, CuP = postcubital, M = median vein, R = radial veins, Sc = subcostal vein.

Holotype. In.53983; Birchi nodule, Black Ven, Charmouth, Dorset. Jackson colln. Dimensions: 26 mm (slightly incomplete) × 5 mm. Wing length estimated 28 mm.

Discussion. Sharov (1968) considered *Ferganopterus* Sharov, from the Lower Lias of Asia, as the most primitive of the family. *O. ornatum* broadly resembles this species and (whether considered primitive or not) both have a highly specialized venation. *Orichalcum* can be distinguished from *Ferganopterus* by having three or four anal veins and a longer branched costal vein. The fusion of the radial sector with the anterior median vein occurs in many of the fossil Oedischiidea. Amongst the Dorset Lias Orthoptera, *Orichalcum* is unique in having a slender wing and relatively simple cubital venation. Some of the patterning has been preserved on the wing and the type of preservation indicates that the forewing was probably strongly sclerotized.

O. ornatum was amongst the last of the specialized triassomantids which arose in the early Trias and extended into the Jurassic. It is one of the few insects to be found in the Birchi nodules from the Turneri Zone of the Dorset Lias, and by one ammonite subzone (perhaps 300,000 years) is older than the insects from the Obtusum Zone, from which the majority of Dorset Lias insects were collected.

Superfamily **GRYLLIDEA**

Family **HAGLIDAE** Sharov, 1968

Sharov (1968) separated the Haglidae from the Gryllidae by the position of the posterior medial and anterior cubital veins. In the Haglidae the post-medial and anterior cubital are displaced to the posterior margin of the wing, whereas in the Gryllidae they are in the middle of the wing, almost parallel to the wing margin. In the gryllids, apart from the characters mentioned, the presence on the forewings of the mirror and associated sound-producing organs and the characteristic sharp curvature of the forewing, which produces the box-like cover of the hindwings and body, are distinctive. These synapomorphic characters indicate that the Gryllidae are a reasonably homogeneous and monophyletic group. The species that remain in the Superfamily Gryllidea, when the Gryllidae *s. str.* are removed, are broadly covered by Sharov's Haglidae; this is almost certainly a polyphyletic group, containing both true close relatives of *Hagla* and also probably stem-group gryllids. However, for the purpose of this faunal study, the species which do not fall into the Gryllidae *s. str.* are placed in the Haglidae, with the proviso of the polyphyletic nature of this group.

Genus ***HAGLA*** Giebel, 1856

Hagla cf. ***gracilis*** Giebel

cf. 1856 *Hagla gracilis* Giebel: 264.

In.59167 is an incomplete specimen which is similar to *H. gracilis* Giebel from the Lower Lias of Gloucestershire. The subcostal vein and radial sector are close together and there are strong cross-veins in the cubital and anal areas; these cross-veins are often curved. The wing is folded and no exact comparison has been possible with the described species of *Hagla*.

Genus ***REGIATA*** nov.

TYPE SPECIES. *Regiata scutra* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Grylloids with strongly pitted forewings. M and Cu parallel near the base. MA curving sharply forward. Subcostal veinlets sinuous.

NAME. 'Bordered'.

Regiata scutra sp. nov.

Figs 17–20

DIAGNOSIS. As genus.

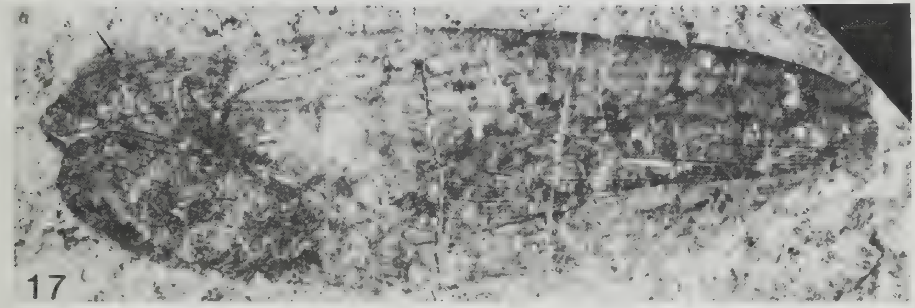
NAME. 'A salver'.

DESCRIPTION. Forewing with short costal vein near base in broad costal/subcostal area. Subcostal vein reaching well beyond middle of wing, subcostal area broad in basal half; subcostal veinlets strongly marked with pits. R almost parallel to Sc for much of its length. M curving strongly towards hind margin before dividing into MA and MP. MA curves forward, MP curves backwards parallel with Cu to wing margin. Anterior branches from MP arise almost at right angles to it. Apical part of median and cubital veins clearly parallel and slightly curved (easily distorted in fossilization). Apex of wing narrower. Anal area very strongly punctate, reticulations clear. Size range: 16·7–21·5 × 6·3 mm.

HOLOTYPE. In.64027 (Fig. 17); Flatstones, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 21·4 × 6·3 mm.

PARATYPES. In.49568, In.49597, In.59146 (Fig. 19), In.59169 (Fig. 20), In.64007 (Fig. 18), In.64037.

17



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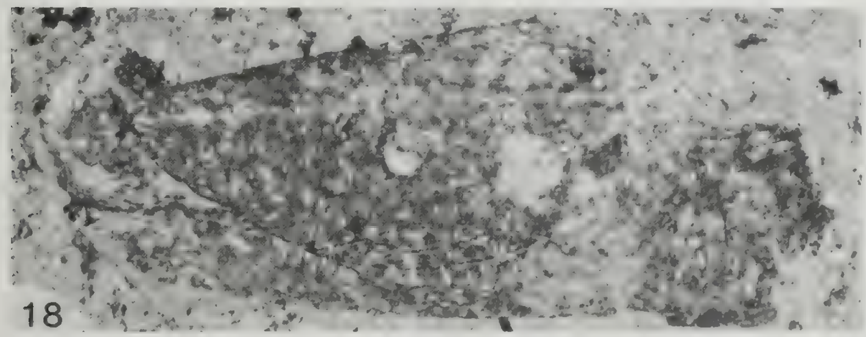


Figs 17–18 *Regiata scutra* sp. nov. (Orthoptera). Fig. 17, **holotype,** In.64027, forewing, 21 mm long. Fig. 18, paratype, In.64007, forewing.

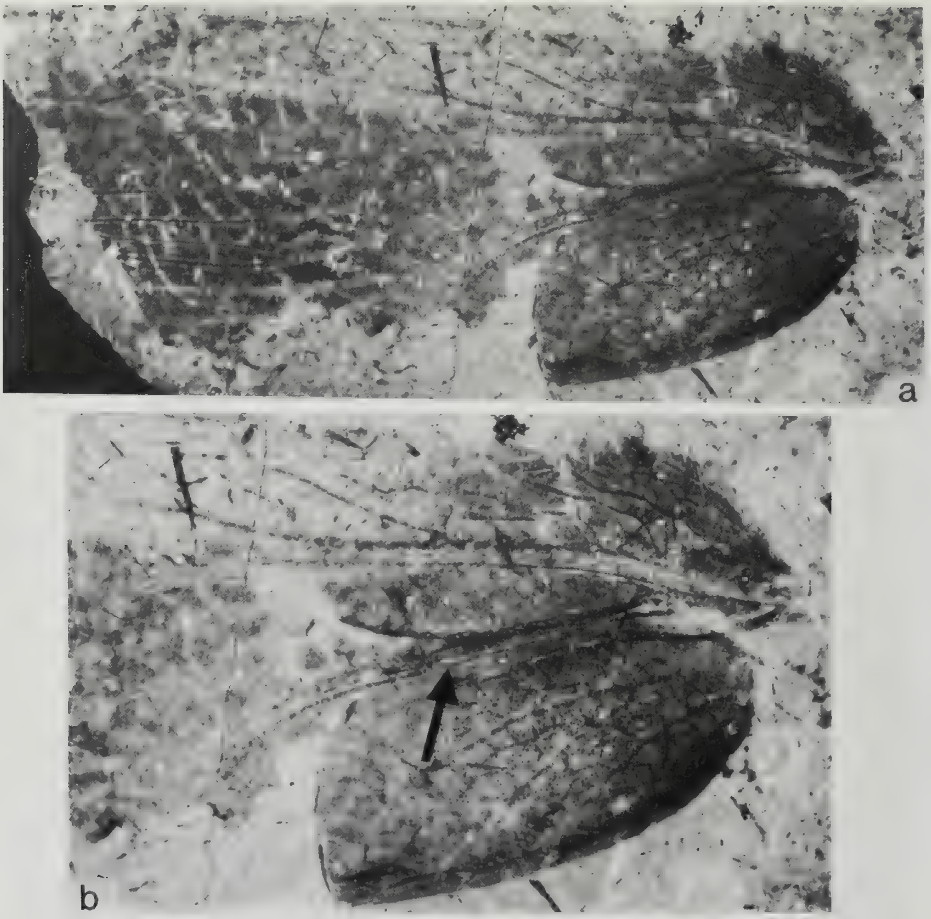


Fig. 19 *Regiata scutra* sp. nov. (Orthoptera). Paratype, In.59146, forewing. b, enlargement of anal area and wing base. Note break in wing in front of anal area (arrowed) caused when the curved wing was flattened. Wing membrane heavily spotted.

OTHER MATERIAL. In.59392.

DISCUSSION. This species is similar to the grylloid *Karataogryllus gryllotalpiformis* Sharov, from the Jurassic of Asia, but differs in the shape of the median vein and the very sinuous subcostal vein. *R. scutra* was probably similar to Recent gryllids where the wings are folded over the back. When these were flattened during fossilization they split at the base of the wing, seen in Fig. 19b (arrow) as a fine break between the anal area and the rest of the wing. *R. scutra* also had the apex of the wings rolled together or even curled up as shown by In.64007 (Fig. 18). When the surface of the rock is wet the fossil appears to be covered in granules which, when examined dry, are seen to be tiny pits. Although these pits are denser in the anal area they occur over most of the forewing. The pitting shows up clearly in the subcostal area where they are arranged regularly along the subcostal veins. The anterior median and postcubital veins on some specimens are thickened; these thickened veins were almost certainly slightly raised above the wing and may have formed part of the stridulatory mechanism, but there is no sign of the mirror which, in Recent forms, is bounded by CuP and a branch of CuA. Vein 1A, which is also part of the stridulatory mechanism in Recent species, is, however, prominent in the fossil. *R. scutra* can be distinguished from *Hagla gracilis* Giebel, which is common in some Lower Lias

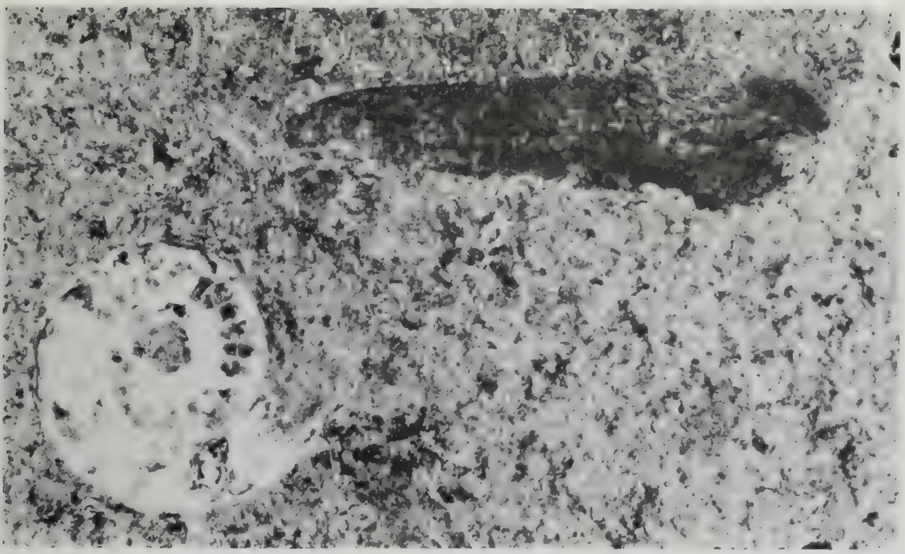


Fig. 20 *Regiata scutra* sp. nov. (Orthoptera). Paratype, In.59169, wing, 27 mm long. This is on the same bedding plane as an ammonite.

deposits in Britain, by a number of characters. The displacement of the postmedian and anterior cubital veins towards the posterior margin occurs in both *Hagla* and *Regiata* but they differ considerably in the form of the subcostal veins and the arrangement of the anal veins. *R. scutra* has a less complex, though equally broad, costal area similar to *H. gracilis*, but the median and cubital veins are nearly parallel towards the apex, suggesting a rolled or curved apex to the wing. The split apparent in most of the fossils between the anal area plus Cu + M and the rest of the wing is consistent with the flattening of the wing in life, which could have been held in the typical gryllid-like (box-like) fashion over the body. Until further studies are made of the Haglidae *s. lat.* the classification of *Regiata* as a haglid must remain provisional (see p. 130).

Genus ***PROTOHAGLA*** Zeuner, 1962

TYPE SPECIES. *Protohagla langi* Zeuner, by original designation. Lower Lias, U.K.

Protohagla langi Zeuner, 1962
Fig. 22

1962 *Protohagla langi* Zeuner: 165; pl. 26, figs 1, 2.

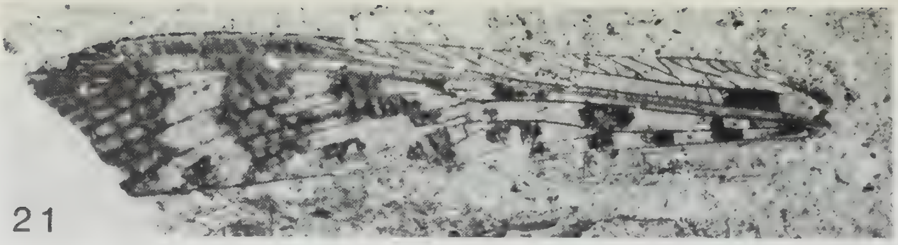
No new material of this species has been found since Zeuner originally described it. *P. langi* is a large insect and had a wingspan of about 150 mm. Zeuner (1962: 166) said that in this specimen (In.59018) the fore and hind wings had been nipped off simultaneously at their bases. He speculated that this had happened when the insect was caught, with the wings closed, by a predator over the land. However, examination shows that the underlying wing is another forewing, so Zeuner's hypothesis is untenable.

Family **GRYLLIDAE** Latreille, 1802

Genus ***PROTOGRYLLUS*** Handlirsch, 1906

TYPE SPECIES. *Protogryllus dobbertinensis* (Geinitz 1880), by subsequent designation of Zeuner (1939: 188). Lias, Europe.

DIAGNOSIS. Gryllids with distinct harp in male forewing but without mirror (Handlirsch 1906: 424).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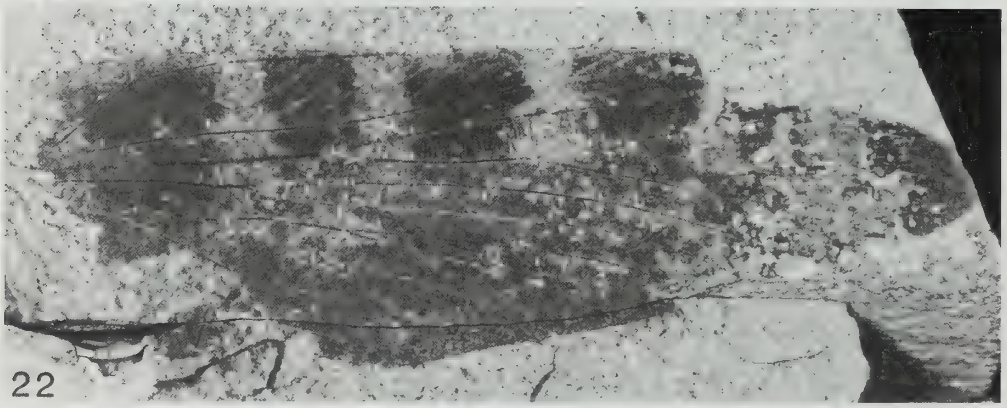
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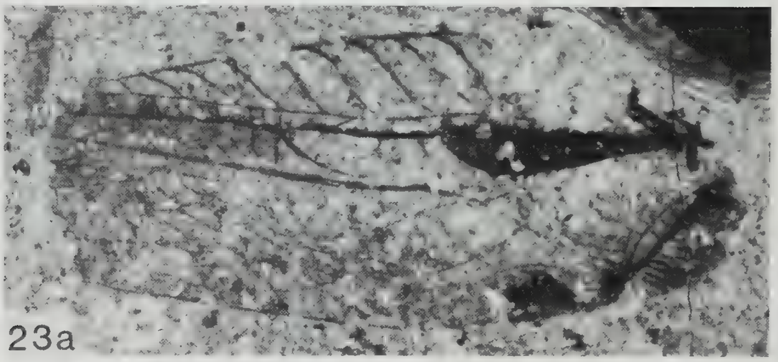
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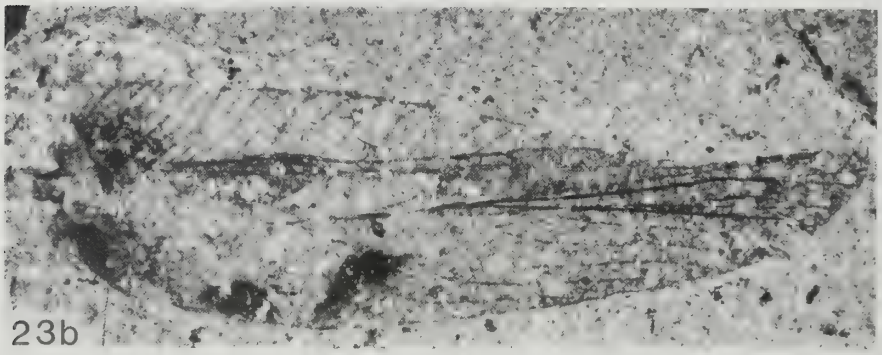

23b

Fig. 21 *Orichalcum ornatum* gen. et sp. nov. (Orthoptera). **Holotype,** In.53983, forewing, 26 mm long. Note the patterning on the wing.

Fig. 22 *Protohagla langi* Zeuner (Orthoptera). Holotype, In.59018, forewing, 61 mm long.

Fig. 23 *Protogryllus magnus* Zeuner (Orthoptera). In.51016, forewing, 26 mm long. a, part. b, counterpart.

Protogryllus magnus Zeuner, 1937
Fig. 23a, b

1937 *Protogryllus magnus* Zeuner: 155.
1939 *Protogryllus* (*Archaegryllodes*) *magnus* Zeuner; Zeuner: 192.

Zeuner based the description of *P. magnus* on two incomplete male specimens, the holotype from the Upper Lias of Dumbleton, Gloucestershire and a second specimen from the Lower Lias of Binton, Worcestershire. Only slight differences have been found between these and the Dorset specimens. The curvature of the median vein, where it curves forward towards the radial, is more gentle in the Dorset specimens than in the holotype. Otherwise the size and rest of the venation are similar. Zeuner's figure of 22 mm wing length is based on the holotype and is probably an underestimate; even so, the Dorset specimens are larger and with the difference in localities, may represent a distinct species.

Zeuner (1937) placed *P. magnus* in the subgenus *Archaegryllodes* Haughton (1924) on the basis of the median and radial veins touching in the forewing. He likened it to a Triassic species, *A. stormbergensis* Haughton from South Africa. In 1939 Zeuner suggested that *Protogryllus grandis* Zeuner might be the female of *P. magnus*, but no further evidence for this hypothesis has been elicited from the Dorset specimens. There is more of the very specialized venation preserved in the Dorset specimens than in the holotype of *P. magnus*; the stridulatory area of the male forewing can be seen in Fig. 23a.

MATERIAL. In.44003, In.51016 (Fig. 23), In.51022, In.59373. Dimensions: 26·7 × 7·4 mm.

Genus ***MICROMACULA*** nov.

TYPE SPECIES. *Micromacula gracilis* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Gryllids with narrow wings, dense maculations. Anal area more extensive than subcostal area. Distinct fan present between Cu and M in centre of wing.

NAME. 'Small spot'.

Micromacula gracilis sp. nov.
Figs 24–25

DIAGNOSIS. As genus.

NAME. 'Slender'.

DESCRIPTION. Forewing with broad base, narrowing apically. Subcostal area reticulate; subcostal vein reaching costal margin well before middle of wing. Costal margin with distinct hump on basal part. Radial vein running roughly parallel to median vein along wing. Cu sharply angled along edge of anal area with CuP close and three anal veins. Whole wing covered with fine spots. Cubital with fan-shaped arrangement of branches to medial veins. Anal area larger than subcostal area, strongly reticulate and covered with spots.

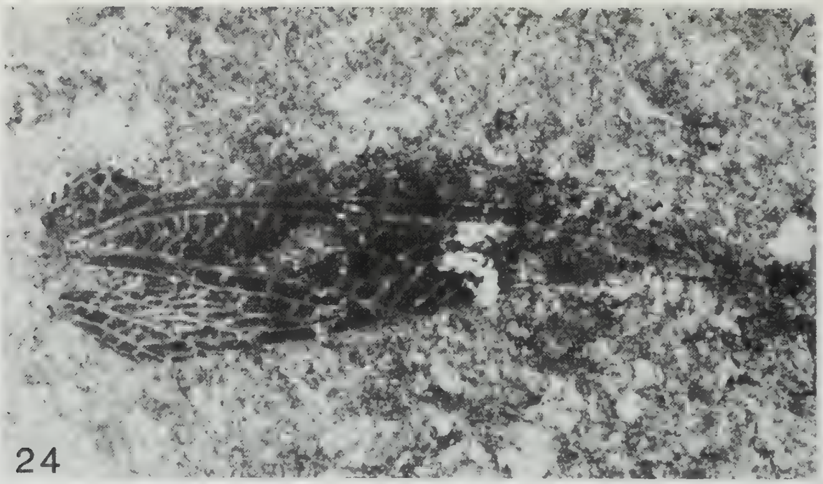
HOLOTYPE. In.49230 (Fig. 24); Birchi nodule, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 11 × 2·6 mm, forewing; 12–13 mm, hindwing.

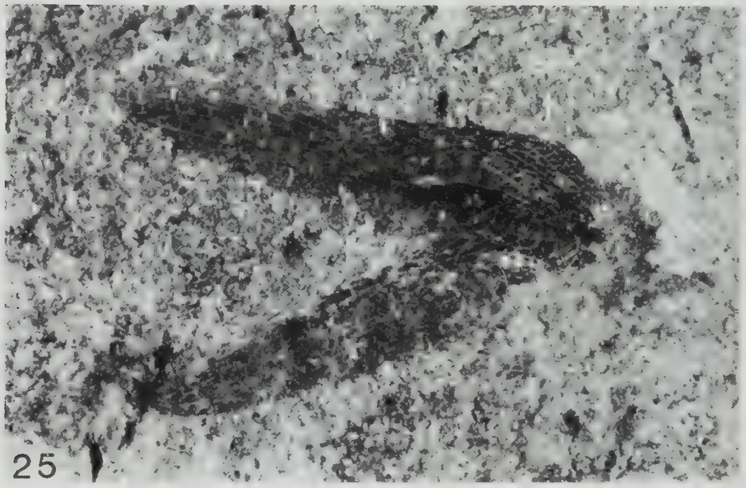
PARATYPES. In.49594, In.51041, In.53913, In.53934, In.53969, In.59126 (Fig. 25).

OTHER MATERIAL. In.53926, In.53973, In.64031.

DISCUSSION. The holotype of *M. gracilis* is from the Turneri Zone whereas most of the paratypes are from the younger Obtusum Zone. This is the only species certainly known to occur in both the Turneri Zone and Obtusum Zone, but for most species zonal age data is unavailable (see p. 110).

Specimen In.59126 (Fig. 25) has both forewings and part of the hindwings preserved. The hindwing is longer than the forewing and is membranous, but is heavily folded and no details of the venation can be seen. The forewings are strongly sclerotized and similar to those of many





Figs 24–25 *Micromacula gracilis* sp. nov. (Orthoptera). Fig. 24, **holotype,** In.49230. Fig. 25, paratype, In.59126, pair of forewings, length 11 mm.

Recent species. The wing was evidently curved round the body in life, as in modern gryllids, because the flattened fossil shows cracks in the position of original folds. *M. gracilis* was probably similar in appearance to the Recent species *Amsurgus lateralis* Chopard (Gryllidae, Trigonidiinae), a cricket from the Pacific area. The forewings of the Recent species are broadly patterned giving a reticulate appearance, and the surface is covered with small spots; these are larger on the veins, and from them hairs arise. Little is known of the biology of the Recent species, which is considered to be typically tree-dwelling, rather than ground-living.

Suborder **CAELIFERA**

Superfamily **LOCUSTOPSIDEA**

Family **LOCUSTOPSIDAE** Handlirsch, 1906

Genus ***LOCUSTOPSIS*** Handlirsch, 1906

TYPE SPECIES. *Locustopsis elegans* Handlirsch, by subsequent designation of Cockerell, 1915. (Handlirsch 1906: 421; Zeuner 1942: 8; Sharov 1971: 90–97). Trias–Upper Lias, Europe.

DIAGNOSIS. CuA divides into three branches. Sc extends almost to apex of wing. R and M run separately to base of wing. M with three, rarely two, branches.

Locustopsis spectabilis Zeuner, 1942
Figs 26–28

1942 *Locustopsis spectabilis* Zeuner: 8; fig. 1.

TYPE LOCALITY. Strensham, Worcestershire; Upper Trias.

DISCUSSION. This species was described by Zeuner on the basis of a single, slightly folded, forewing from Strensham and he mentioned a possible second specimen from Warwickshire. There are a number of specimens from Dorset which I attribute to this species, although they differ slightly from the holotype in the relative proportions of the wing; this could be due to the slight folding in the holotype. The Dorset specimens show a weakly-developed precostal vein while the actual costal vein is well developed with lateral branches. The subcostal vein reaches the wing tip while the radial, subcostal, median and cubital veins are separated almost to the base of the wing. The median vein divides into three branches; in some specimens the third branch comes off the postmedial while in others it comes off the antemedial. Most of the specimens from Dorset, and the holotype from Worcestershire, have a three-branched cubital vein, but two Dorset specimens (In.49591, In.51043 (Fig. 28)) have an extra branch, making a four-branched cubital. Recent Orthoptera have considerable intraspecific variation in wing venation (Ragge 1955) but, in Recent species, a four-branched cubital is unusual. The rest of the venation of these two specimens is similar to the other Dorset specimens and they are considered to be merely intraspecific variants.

MATERIAL EXAMINED. In.49203, In.49208, In.49565 (Fig. 26), In.49586, In.49591, In.49593 (Fig. 27), In.49600, In.49614, In.50992, In.51001, In.51035, In.51043 (Fig. 28), (? In.53900), In.53908, In.53914, In.53917, (? In.53984), In.59121, In.59131, In.59357, In.59358A, In.59367, In.64039.

DIMENSIONS. 22–29 mm.

Order **PHASMATODEA**, stick-insects

Superfamily **XIPHOPTERIDEA**

Family **AEROPHASMATIDAE** Martynov, 1928

This family was based originally on specimens from the Jurassic of Karatau. Sharov (1968) commented on traces of dense short hairs on these specimens, which are also clearly visible on the new species from Dorset.

Genus ***DURNOVARIA*** nov.

TYPE SPECIES. *Durnovaria parallela* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Elongate wing with roughly parallel veins. Costal vein simple, unbranched; costal area densely hairy. Median three-branched with MP and Cu having a common stem.

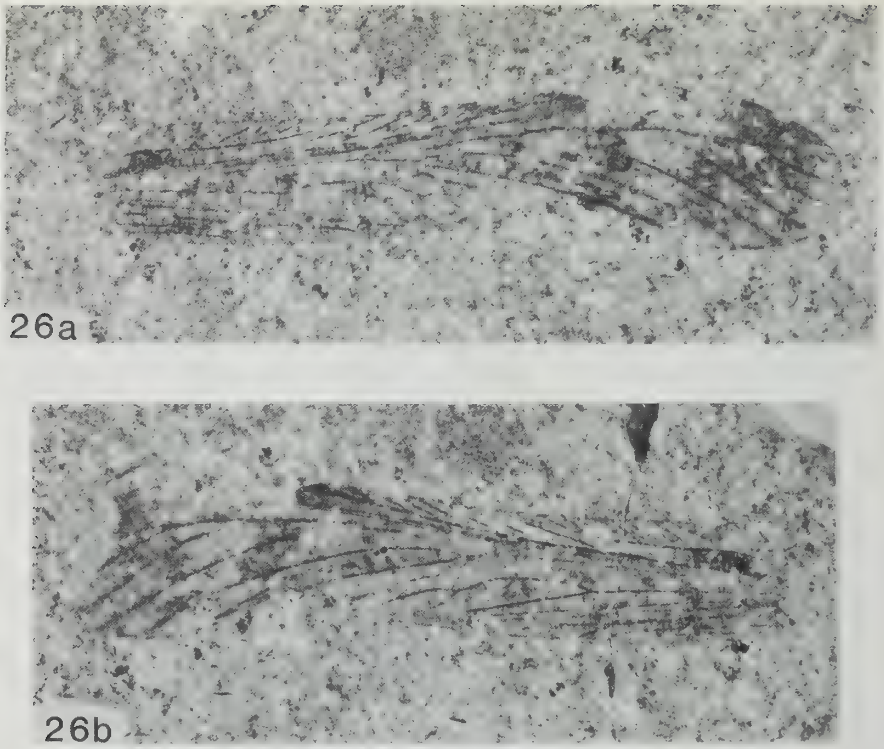
NAME. Latin name of Dorchester.

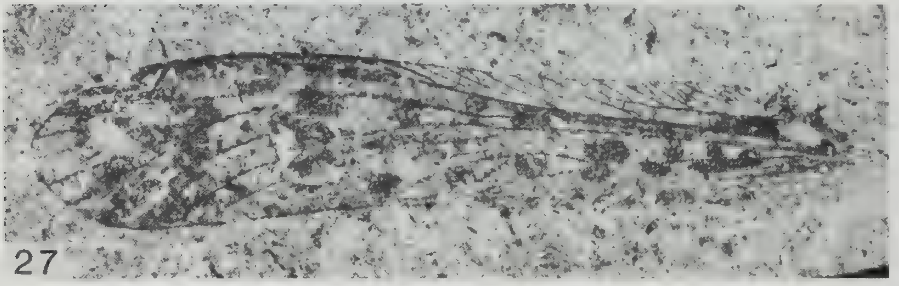
Durnovaria parallela sp. nov.
Figs 29, 33–34

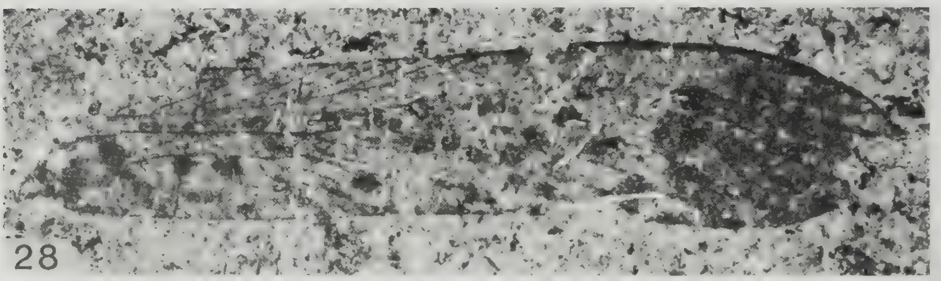
DIAGNOSIS. As genus.

NAME. 'Parallel'.

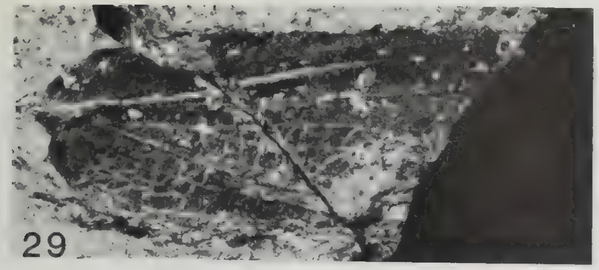
DESCRIPTION. Precostal, costal and much of subcostal areas very hairy, rest of wing strongly pigmented and probably hairy. Sc short, reaching to costal margin approximately level with first fork of radial vein. Four radial veins (plus radial sector) almost parallel along wing. Median and radial veins clearly fused at base of wing. Median (strictly M + CuA) divides very early into MA, which again forms three branches, and MP/Cu branch. The latter divides into

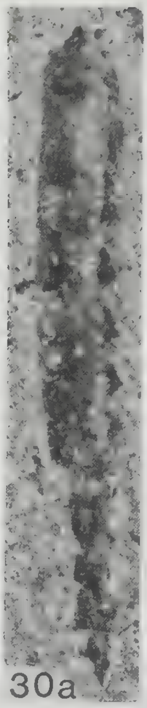


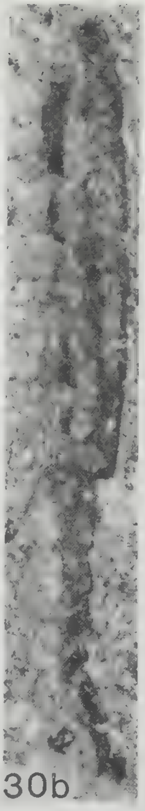


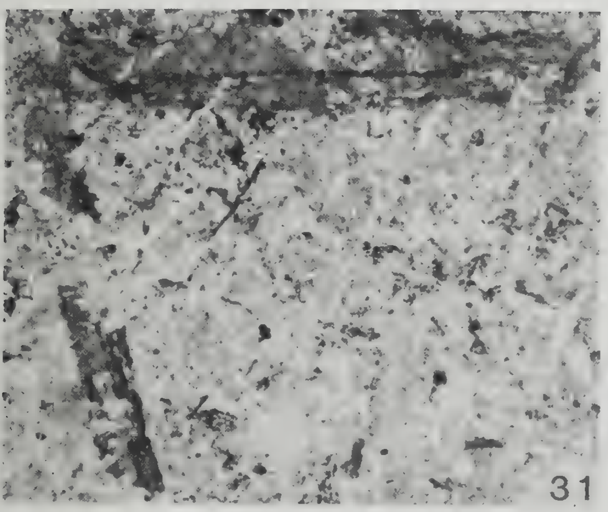


Figs 26–28 *Locustopsis spectabilis* Zeuner (Orthoptera). Fig. 26, In.49565, forewing, 24 mm long. a, part. b, counterpart. Fig. 27, In.49593, forewing. Fig. 28, In.51043, forewing.









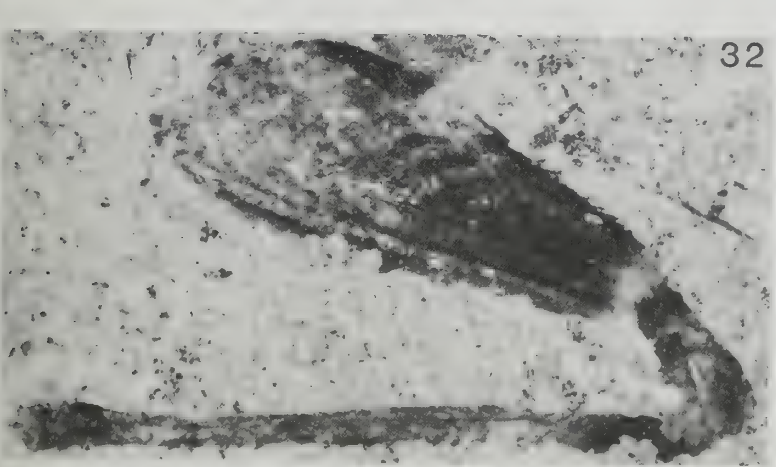


Fig. 29 *Durnovaria parallela* gen. et sp. nov. (Orthoptera). **Holotype,** In.59171, counterpart. See Fig. 33.

Figs 30–32 Orthoptera, saltatoria-type legs. Fig. 30, In.59127, tibia and tarsi, total length 24 mm. Stout spines on tibia. a, part. b, counterpart. Fig. 31, In.59391, femur 10·9 mm, tibia 10 mm. Note ridge of spines along both. Fig. 32, In.53919, femur 9·2 mm.

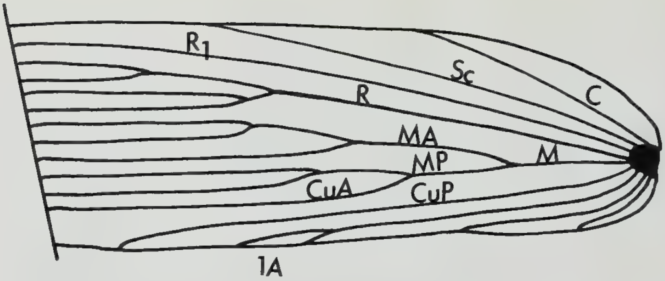


Fig. 33 *Durnovaria parallela* gen. et sp. nov. (Orthoptera). Diagram of forewing venation. A = anal area, C = costal vein, Cu = cubital veins, M = median veins, R = radial veins, Sc = subcostal vein.

two, a postmedial and anterior cubital. The posterior branch of M + Cu forms CuA. CuP comes off near the base of M from the common stem of M + CuA and runs unbranched to the wing margin. The first anal has a short apical branch, the second is nearly as long but unbranched, while the third is short. There are many small reticulations in the area between 2A and the wing margin.

HOLOTYPE. In.59171 (Figs 29, 34); Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 34 × 7·7 mm; estimated wing length 36 mm.

DISCUSSION. This species is separated from the Chresmodidae (*sensu* Sharov, 1968) by the branching of the postmedian and anterior median veins. It differs from *Aerophasma* Martynov in having a weakly-developed cubital vein and in the division of the anterior median vein into two branches. The long parallel-vein appearance is typical of the Xiphopteroidea. The very hairy nature of the wing, particularly clear in the anterior basal part of the wing, is characteristic of the Aerophasmatidae, a family currently known from the Jurassic of the U.S.S.R. The other families in the Xiphopteroidea are Triassic (Xiphopteridae, Aeroplanidae), Jurassic (Necrophasmatidae) or Cretaceous (Cretophasmatidae). All are regarded as related to, though not necessarily direct ancestors of, modern stick-insects (Phasmidae).

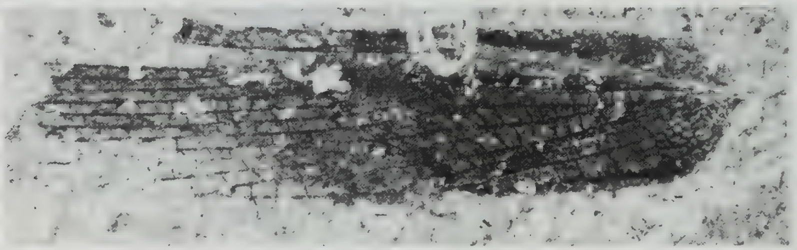


Fig. 34 *Durnovaria parallela* gen. et sp. nov. (Orthoptera). **Holotype,** In.59171, part, forewing, 34 mm long. See Fig. 29.

Order **HEMIPTERA**, plant bugs

Suborder **HOMOPTERA**

Six homopterous insects occur in the Jackson collection. Three of these are considered to belong to a species in the Cicadidea, one is unidentifiable but in the same superfamily, one is placed in the Cicadellidea and the last is in the Superfamily Fulgoridea. Currently there are six species of Mesozoic Homoptera known from the U.K.; these are three species of *Margaroptilon* (Handlirsch 1906) and one of *Homopterites* (Handlirsch 1906); both genera are in the Cicadellidae, one in Tettigarctidae and one in Cicadidae (Whalley 1983).

Superfamily **CICADIDEA**

Family **TETTIGARCTIDAE** Bekker-Migdisova, 1949

There are only two living species of this family which is common in the fossil record from the Triassic onwards. Species of several genera are known from the Mesozoic while the sister-group, Cicadidae, are rare in the Mesozoic (Whalley 1983). The fossils from Dorset, which have similar venation to *Shuraboprosbole* Bekker-Migdisova, are very much smaller. The vein which represents the base of the median, linking it and the anterior cubital to the postcubital as a cross-vein, cannot be seen in the Dorset specimens and was probably not present.

Genus ***PARAPROSBOLE*** nov.

TYPE SPECIES. *Paraprosbole rotruda* sp. nov. Lower Lias, Dorset, U.K.

DIAGNOSIS. Base of M + CuA thickened and curved. Cross-vein from M + CuA missing.

NAME. Like *Prosbole*, but distinct.

Paraprosbole rotruda sp. nov.

Figs 35–36

DIAGNOSIS. As genus.

NAME. A genus of Recent moths (Heinrich 1956: 225).

DESCRIPTION. Base of M + CuA curved and thickened. R clearly divided as far as nodal line. CuA and anal veins unbranched. Nodal line double, pigmented.

HOLOTYPE. In.59374 (Fig. 35); Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: Base of wing to nodal line 12–13 mm. Nodal line, from anterior to posterior wing margins, 8–9 mm. Total wing length 20–22 mm.

PARATYPES. In.48162 (Fig. 36), In.64395.

DISCUSSION. None of the wings is complete but comparison of the base of the wing (holotype) and the width of the wing at the nodal line with all the specimens suggests they are all conspecific, even though one is represented only by the apical part of the wing. They differ from the Triassic *Cicadoprosbole* in having fewer short branches on the radial vein near the apex of the wing. In specimen In.48162 (Fig. 36) the ambient vein is clear, with traces of the membrane distal to this visible.

Tettigarctidae, gen. et sp. indet.

The single specimen is incomplete and cannot be identified further than to family. It has a clearly preserved nodal line and parts of a few apical veins can be seen. There are some strongly marked sclerotized areas towards the centre of the front margin of the wing but the whole wing is much smaller than in *Paraprosbole*.

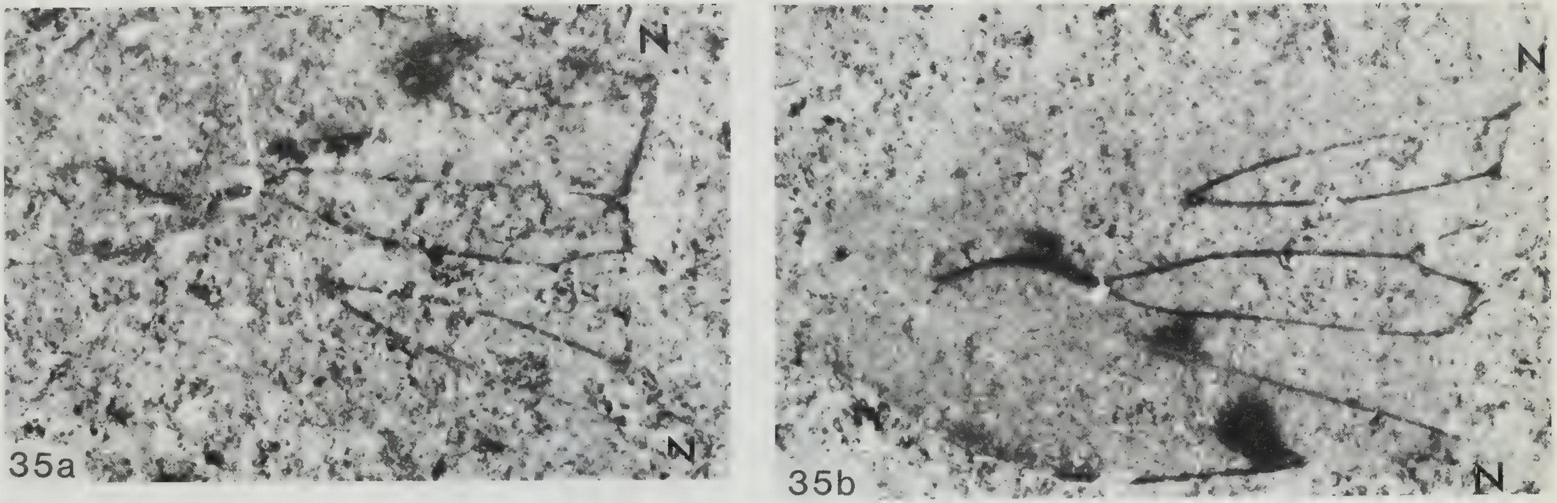
MATERIAL. In.51011 (not figured). Dimensions: Apical vein *c.* 4·5–5 mm. Nodal line *c.* 4·5 mm. Basal part of wing to nodal line *c.* 7·5 mm.

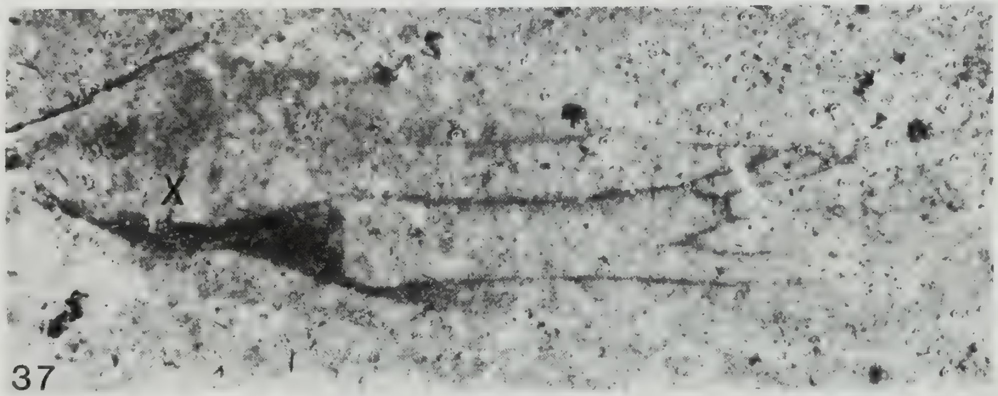
Superfamily **CICADELLIDEA**, gen. et sp. indet.

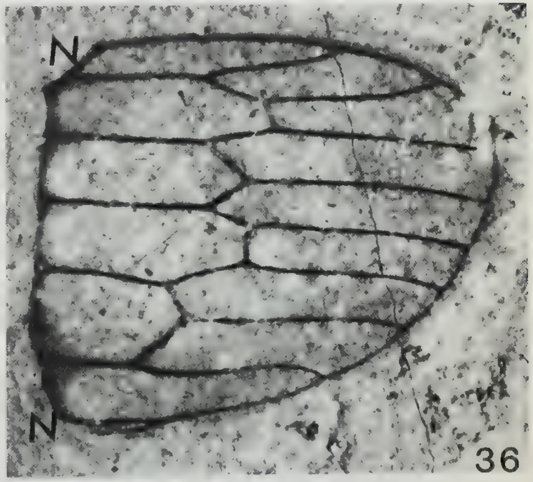
Fig. 37

The single specimen does not have the nodal line as clearly preserved as in the Tettigarctidae but has a strongly curved R + M + Cu. Some of the apical veins are preserved.

MATERIAL. In.49225. Dimension: Wing length *c.* 8 mm.







Figs 35–36 *Paraprosbole rotruda* gen. et sp. nov. (Homoptera). Fig. 35, **holotype,** In.59374. N-N marks position of nodal line, which is about 8 mm long. a, part. b, counterpart. Fig. 36, paratype, In.48162. N-N = nodal line, approx. 8 mm long.

Fig. 37 Cicadellidea, gen. et sp. indet. (Homoptera). In.49225. X = base of radial + medial + cubital veins. Wing approx. 8 mm long.

Superfamily **FULGORIDEA**

Family **CIXIIDAE** Spinola, 1839

Genus ***MESOCIXIELLA*** Martynov, 1937

TYPE SPECIES. *Mesocixiella asiatica* Martynov, by original designation. Upper Triassic and Lower Jurassic, U.S.S.R.

Mesocixiella* (?) *fennahi sp. nov.

Fig. 38

DIAGNOSIS. Fulgoroid with short branches to R_2. Front margin of tegmina straight.

NAME. After Dr R. G. Fennah, specialist in Fulgoroids.

DESCRIPTION. Head regularly curved, narrow. Rostrum reaching to metathorax. Sc vein long, R probably unbranched near apex. Two wings overlap and some of the veins visible in the figure are from the lower wing. M forks with several more apical forks. Eyes just visible, trace of antenna below eye.

HOLOTYPE. In.53942; Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Head to tip of wing, 5·9 mm; Wing approx. 4 mm. Head to tip of abdomen, 3·7 mm.

DISCUSSION. I am grateful to Dr R. G. Fennah for comments on this specimen in which he indicated the general cixiid-like appearance, although pointing out that some of the diagnostic features cannot be seen. Cixiids are an extant group with a long fossil history from the Permian (Rohdendorf 1962). *M.* (?) *fennahi* is only provisionally placed in the genus *Mesocixiella*.

Suborder **HETEROPTERA**

The Heteroptera are currently the subject of a joint research project by the present author with W. R. Dolling and Y. I. Popov. The paper (in press) will contain a detailed taxonomic account of the new species and a discussion of their affinities. The basic information from this study will be summarized here for use in the evaluation of the fauna.

Thirty specimens of Heteroptera from the Dorset Lias occur in the Jackson collection, and one additional specimen from the same locality is preserved in the City of Bristol Museum and Art Gallery.

The results of the study showed that, while there were aquatic Heteroptera which could be placed in Recent families, all the terrestrial species belonged to extinct families. This confirms similar results with the Heteroptera from the Upper Lias of Germany found by Popov & Wootton (1977), where they were unable to place any of the terrestrial species in extant families. In the forthcoming revision of the Heteroptera of the Dorset Lias, one species is placed in Archegocimicidae, eight in the Pachymeridiidae, two in the Corixidae, and four (including the specimen from the Bristol Museum) in the Belostomatidae. Of the remaining 15 specimens, 14 are placed in the Infraorder Cimicomorpha and will be put in a new family, while the remaining specimen is in the Infraorder Leptopodomorpha and will also be placed in a new family. The proposed names for the various taxa which will appear in the joint paper are not given here to avoid nomenclatural complications, but the registration numbers will allow correlation between the general discussion here and the subsequent descriptions of these species in the joint paper.

Infraorder **CIMICOMORPHA**

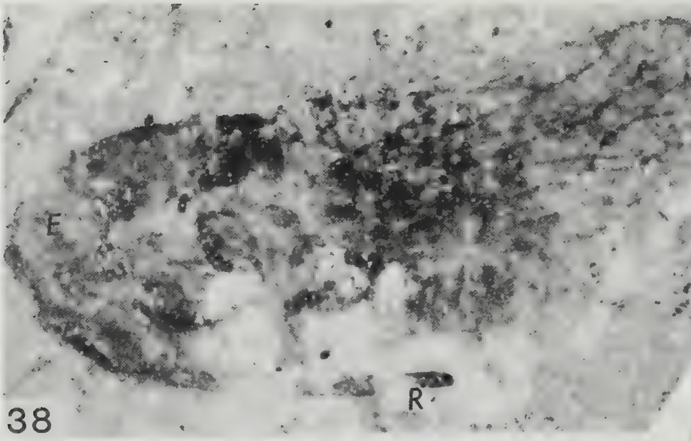
Family **ARCHEGOCIMICIDAE** Handlirsch, 1906

Archegocimicidae, gen. et sp. indet.

In.51007 is part of a wing which is provisionally referred to this family.

Family nov. 1

This family is erected to include the series of 14 specimens, all with clear cuneal and medial fractures and with the head, thorax and abdomen covered with short curved bristles.



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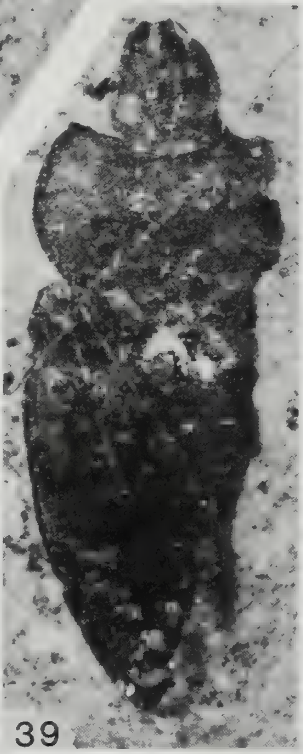

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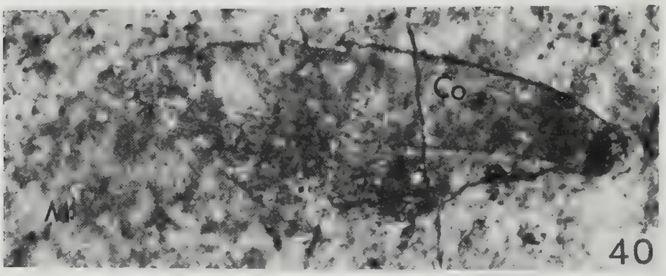

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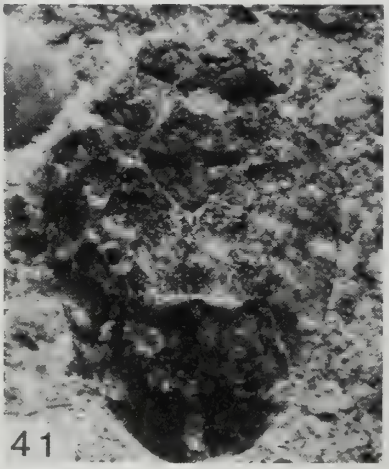

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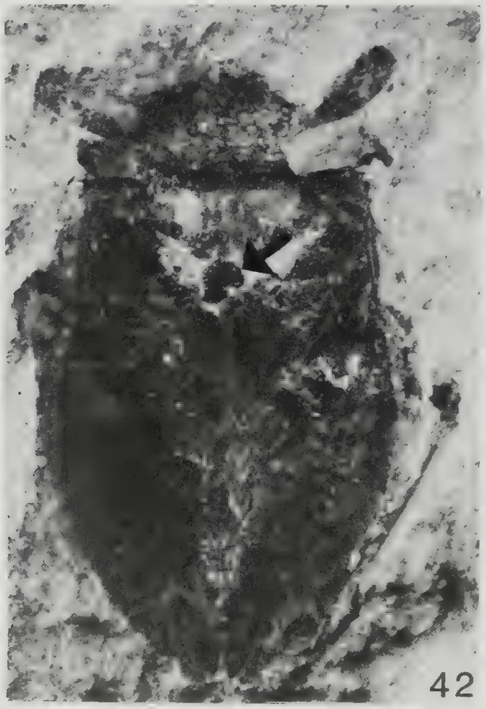


42

Gen. et sp. nov. 1A

Figs 39–40

Diagnosis. Head elongate, slightly longer than pronotum. Eyes small, hairy. Legs slender, rather short with femora scarcely reaching beyond body margin. Cuneal and medial fracture present. Pronotum strongly transverse, its lateral margins explanate and embracing the head.

Material. Four specimens from Black Ven, nine specimens from Stonebarrow, one specimen from Charmouth. In.49216, In.49243, In.49567, In.49576, In.49589, In.51048, In.53909, In.53986, In.53995, In.59104, In.59128 (Fig. 40), In.59137 (Fig. 39), In.59147, In.59358B. Dimensions: 8·8–10 mm body length. Jackson colln.

Discussion. This is a very distinctive species of Heteroptera with a characteristically shaped head and prothorax, and conspicuous curved setae. Judged on the number of specimens in relation to the total number of Heteroptera in the collection, this species was common in the area from which the Dorset Lias insects were derived.

Infraorder **LEPTOPODOMORPHA**

Family nov. 2

This family is erected for a single species and genus from the Dorset Lias.

Gen. et sp. nov. 2A

Fig. 41

Diagnosis. Pronotum with narrow anterior collar and transverse sulcus dividing it into smaller anterior and larger posterior lobes. Forewing with cuneal and medial fracture; membrane clearly differentiated from corium. Forewings greatly widened in costal area. Pronotum, scutellum, clavus and corium finely punctate.

Material. Black Ven, In.59152. Dimensions: 5·4 × 3·5 mm wing. Jackson colln.

Discussion. Although the head is missing from the single specimen, the rest of the body is sufficiently well preserved to show characters of the new family.

Infraorder **PENTATOMOMORPHA**

Family **PACHYMERIDIIDAE** Handlirsch, 1906

A family with a number of species and genera described from the Mesozoic.

Gen. et sp. nov. 3A

Diagnosis. Forewing narrow, as in *Pachymeridium* Geinitz, but with three branches of the radial vein arising close together near the apex of the medial fracture. Clavus and corium punctate, with cross-markings in 'herring-bone' pattern.

Material. Four specimens from Black Ven, three specimens from Stonebarrow. In.49566, In.51039, In.53901, In.53941, In.59105, In.59151, In.64014. Dimensions: 8–9 mm wing. Jackson colln.

Fig. 38 *Mesocixiella* (?) *fennahi* sp. nov. (Homoptera). **Holotype,** In.53942. R = rostrum, E = eye. Total length of insect including wings 5·9 mm.

Figs 39–40 Gen. et sp. nov. 1A (Heteroptera). Fig. 39, In.59137. Length overall 9 mm. Fig. 40, In.59128, forewing. Co = corium, M = membrane.

Fig. 41 Gen. et sp. nov. 2A (Heteroptera). In.59152. Length of body 5·4 mm.

Fig. 42 Gen. et sp. nov. 8A (Heteroptera). Bristol Museum specimen no. 111/1958. Arrow indicates metathoracic gland. Length of insect 32 mm.

When the Dorset pachymerids in the Jackson collection were examined, several possible new species were separated; these are listed below but although distinct from sp. nov. 3A, they are not sufficiently well preserved for description. All are from the Flatstones, Stonebarrow, Dorset.

Pachymeridiidae species 4A. Material: In.51028. Dimensions: 7·5 mm wing.

Pachymeridiidae species 5A. Material: In.51005. Dimensions: 6·7 mm wing.

Pachymeridiidae species 6A. Material: In.50999. Dimensions: 6·3 mm wing.

Infraorder **NEPOMORPHA**

Family **CORIXIDAE** Leach, 1815

Two specimens of aquatic corixid bugs are ascribed to this family but they are too poorly preserved to warrant a formal description and name.

MATERIAL. 2 specimens from Black Ven, Charmouth; In.59140, In.59166. Dimensions: 9–10 mm × 5 mm body. Jackson colln.

Family **BELOSTOMATIDAE** Leach, 1815

This family of aquatic bugs is represented by three specimens in the Jackson collection and one well-preserved specimen from the same Dorset locality in the City of Bristol Museum and Art Gallery. The Dorset specimens are the earliest known examples of the family, which was evidently well differentiated into a discrete group by the Lower Lias. Most of the specimens show the movable breathing siphon characteristic of this aquatic family.

Genus ***MESONEPA*** Handlirsch, 1906

TYPE SPECIES. *Mesonepa primordialis* Handlirsch (1906: 637), by subsequent designation of Popov (1971: 116). Jurassic, western Europe.

***Mesonepa* species 7A**

DIAGNOSIS. Smaller than other species of *Mesonepa*.

MATERIAL. Two specimens from Stonebarrow, Dorset; In.51014, In.59383. Dimensions: 13 × 6 mm.

DISCUSSION. This is one of the smallest species known in the family but has many of the features typical of Recent species. The scutellum is broad and is a unique feature, suggesting that the earliest belostomatids may have resembled the naucorids.

Gen. et sp. nov. 8A

Fig. 42

DIAGNOSIS. Belostomatids with anterior tarsi and tibia not fused.

MATERIAL. One specimen from Charmouth, Dorset; in City of Bristol Museum and Art Gallery. Dimensions: 32 × 18·5 mm.

DISCUSSION. This species, which looks very similar at first glance to Recent species, differs in the structure of the forelegs. In Recent species the forelegs are modified into grasping organs and the tarsi and tibia are fused together. With this they seize their prey. In the new species the tarsi are free and not fused to the tibia and presumably a slightly different technique for grasping the prey was used. The preservation of the metathoracic gland (Fig. 42, arrowed) shows clearly, but the fact that some of the components were red as in modern species is even more remarkable. A preliminary examination of the contents of this gland has indicated a high sulphur level for the red material and may well indicate the presence of organo-sulphur compounds (see p. 112).

Order **RAPHIDIOPTERA**, snakeflies

Adults and larvae of this order are predatory, feeding on other insects. The Raphidioptera have a long fossil history but the Permian and Upper Carboniferous species which have been ascribed to the order are probably not correctly assigned (Carpenter 1967). There are only about 160 living species in the world, although Carpenter (1967) considered that they were a more diverse group in the Mesozoic. Most of the fossils are known only from the wings (e.g. Carpenter 1936, Martynova 1947, 1961, Macleod 1970) while the characteristically shaped body with elongate pronotum is rarely preserved. Although the exact shape of the prothorax is not clear in the first species described below, it is certainly somewhat elongated.

Family **MESORAPHIIDIDAE** Martynov, 1925*a*

DIAGNOSIS. Subcostal vein ends around the middle of the costal margin. Costal area narrower than in Recent Raphidioptera. Rs originated well before centre of wing.

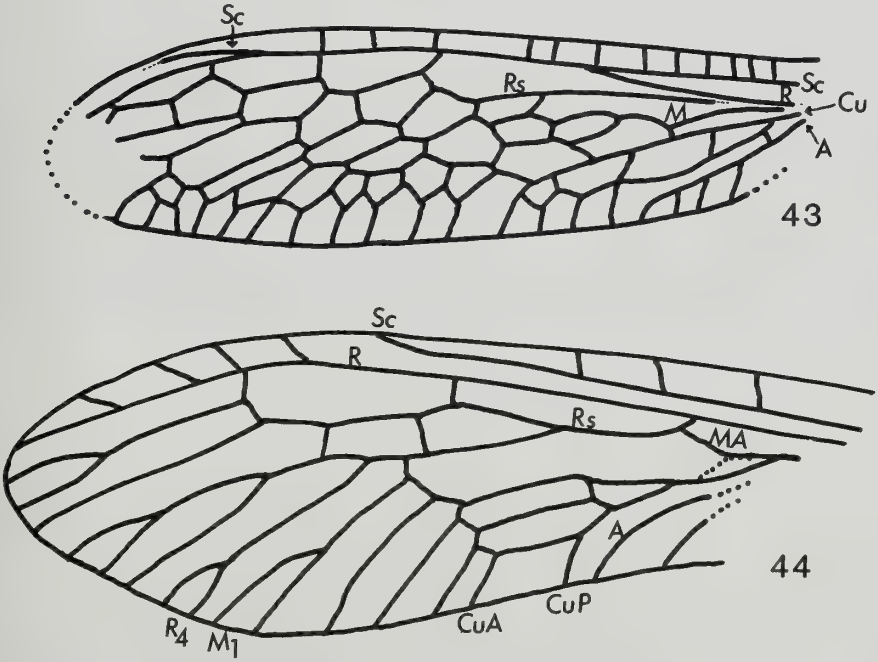
Lower and Upper Jurassic.

Genus ***METARAPHIDIA*** nov.

TYPE SPECIES. *Metaraphidia confusa* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Forewing with two large radial cells between R and Rs. Short pterostigmal cross-veins. Hindwing broadly similar, subcostal vein slightly shorter than in forewing.

NAME. Varied from *Raphidia*.



Figs 43–44 Diagram of wing venations in Raphidioptera. A = anal veins, Cu = cubital veins, M = median veins, MA = anterior median vein, R = radial veins, Rs = radial sector, Sc = subcostal vein. Fig. 43, *Priscaenigma obtusa* gen. et sp. nov. Fig. 44, *Metaraphidia confusa* gen. et sp. nov.

DISCUSSION. The presence of pterostigmal cross-veins differentiates this genus from others in the Mesoraphidiidae. Pterostigmal cross-veins are also found in Recent Raphidiidae but the very elongate radial cells are characteristic of *Metaraphidia*. There are also more marginal branches (8–9) to the radial veins than in other genera of Mesoraphidiidae.

Metaraphidia confusa sp. nov.

Figs 44–45

DIAGNOSIS. As genus. Discal cell small, less than half length of either radial cell.

NAME. 'Mixed up'.

DESCRIPTION. Forewing with hairy costal margin, base of wing obscured. Rs branches off R towards base of wing. Base of M and origins of MA and MP obscured. MP short, probably fused for part of length with Cu. Posterior median cells all broadly similar in shape. Fore and hind wings overlying one another. No trace of pterostigma. Body and head partially obscured. Prothorax longer than width of head. Abdomen slender, tip enlarged.

HOLOTYPE. GSM 117552 (Fig. 45); Charmouth, Dorset; in British Geological Survey collection. Dimensions: Forewing 14·5 × 4·8 mm.

DISCUSSION. This snakefly was evidently washed up against an ammonite and buried with it. Also trapped against the same ammonite was another insect; all three animals were fossilized together. The second insect, probably dipterous but poorly preserved, was fossilized partly under the snakefly (Fig. 45, A–D). Most of the ammonite (A) has been cut away to show the underlying insects, of which the dipterous wing (B) is just faintly visible next to the larger insect. The snakefly head (C) and prothorax (D) are just visible on the specimen but three of the four wings are tightly overlapped and individual details are difficult to discern. Fortunately one forewing is displaced slightly clear of the others.

Family **BAISSOPTERIDAE** Martynova, 1961

DIAGNOSIS. Raphidians with a long or short Sc. Cells in radial and median area of wing more numerous than in Mesoraphidiidae.

Lower and Upper Jurassic.

Genus ***PRISCAENIGMA*** nov.

TYPE SPECIES. *Priscaenigma obtusa* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Raphidians with very long basal radial cell and 3–4 more radial cells to apex of wing. The long basal cell separates this genus from *Baissoptera* Martynova.

NAME. 'Ancient riddle'.

Priscaenigma obtusa sp. nov.

Figs 43, 46

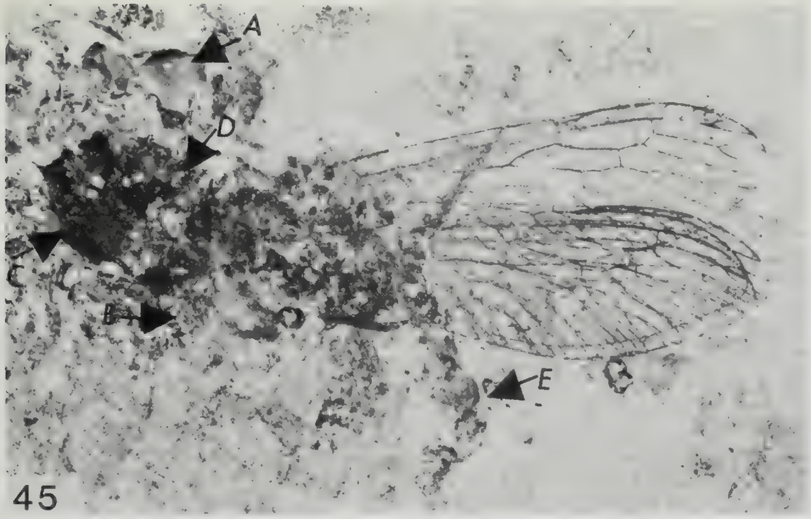
DIAGNOSIS. As genus.

NAME. 'Blunt'.

DESCRIPTION. Forewing, subcostal vein simple, reaching to near wing apex. One basal subcostal cross-vein present (but area distorted and others may be present), pterostigma obscure. M arising off R. Intramedian cell broader apically. CuA roughly parallel to hind margin with 1–2 apical branches. Several rather elongate cells in radial and median areas.

HOLOTYPE. In.53898 (Fig. 46); Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 12·6 mm long.

DISCUSSION. This specimen has been fossilized with its wings together, and as a result it is difficult in one or two places to distinguish the underlying wing veins from those of the top



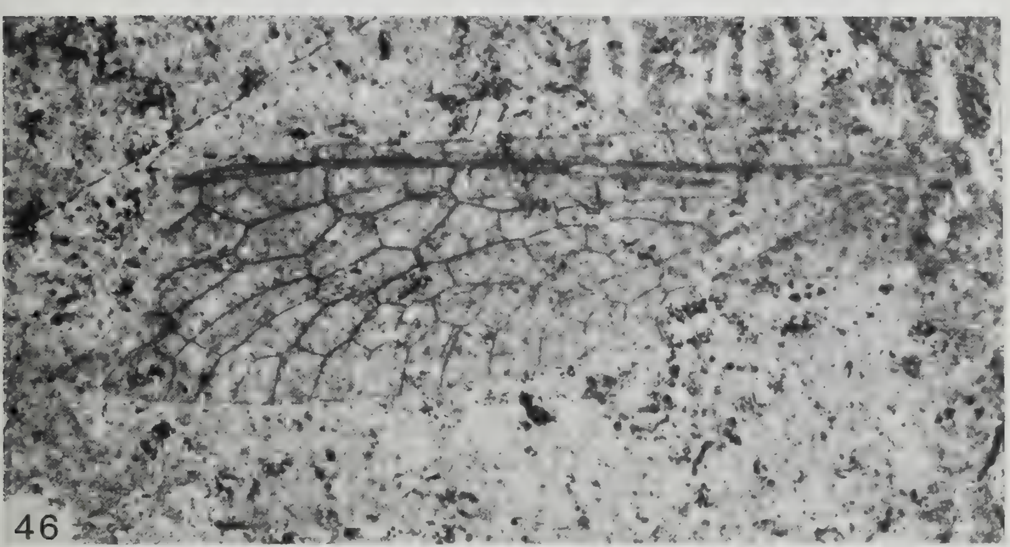


Fig. 45 *Metaraphidia confusa* gen. et sp. nov. (Raphidioptera). **Holotype,** British Geological Survey collection no. GSM 117552. Length of forewing 14·5 mm. The anterior part of the insect body was covered by an ammonite which has been partly removed; there is also a small dipterous specimen below this ammonite. A = ammonite, B = dipterous wing, C = head of *Metaraphidia*, D = protothorax of *Metaraphidia*, E = abdomen of *Metaraphidia*.

Fig. 46 *Priscaenigma obtusa* gen. et sp. nov. (Raphidioptera). **Holotype,** In.53898, forewing 12·6 mm long.

wing. In particular there is a short, indistinct, vein between the subcosta and the costal margin about half-way along the wing. This is almost certainly part of the underlying wing (? a hindwing) and not the subcostal vein of the fore (top) wing. The actual subcosta of the forewing appears to extend almost to the apex of the wing.

Initially this specimen was considered to be a chrysopid (Neuroptera), with some general similarities to the aberrant Recent genus *Kimochrysa* Tjeder, 1966 (Chrysopidae); in particular the long radial cell and the shape of the intramedian cell are similar. However, the origin of the radial sector is atypical of the Chrysopidae and the marginal veins in the fossil are unbranched. The cells in the median/apical area of the wing are more numerous than in the Mesoraphidiidae and are more typical of the Baissopteridae, although the described species of *Baissoptera* Martynova all have shorter subcostal veins. The radial cell in *Priscaenigma* is longer than in *Baissoptera* and the new species may well merit a new family of its own.

Order **MECOPTERA**, scorpion flies

The publication of their bibliography of the Mecoptera by Schlee & Schlee (1976) and of Willmann's (1978) catalogue of fossil Mecoptera has brought together the very scattered literature of this order.

Following Hennig (1981) and other workers, the two main suborders of the Mecoptera, Eumecoptera and Protomecoptera, are accepted here. The Protomecoptera, which are exclusively fossil, have many subcostal veinlets and a modified cubital vein. The vast majority of Recent and fossil species are placed in the Eumecoptera, in which the number of costal veinlets is reduced and the cubital vein is unbranched. Hennig interpreted the cubital vein as a composite one with M_4.

From the Lower Permian into the early Jurassic, Mecoptera fossils are common. They are known from the Lower Cretaceous and into the Tertiary (Willmann 1978) but are far less abundant in the Recent fauna. In the late Triassic and throughout the Jurassic fossil Mecoptera are numerous both as species and individuals, their abundance at this period contrasting sharply with the small size of the Recent fauna, with only about 300 extant species. This is the reverse of the position with, for example, the Diptera or Lepidoptera, which are rare as fossils in the Jurassic but abundant in the Recent fauna.

Recent Mecoptera are mostly carnivorous in adult and larval stages, feeding on insects. Mecoptera do not feed on the wing like dragonflies but hunt for their prey while it rests or feed on dead insects. There is no reason to suppose, from a study of the few preserved mouthparts of fossil Mecoptera, that their feeding habits were any different from those of their living relatives.

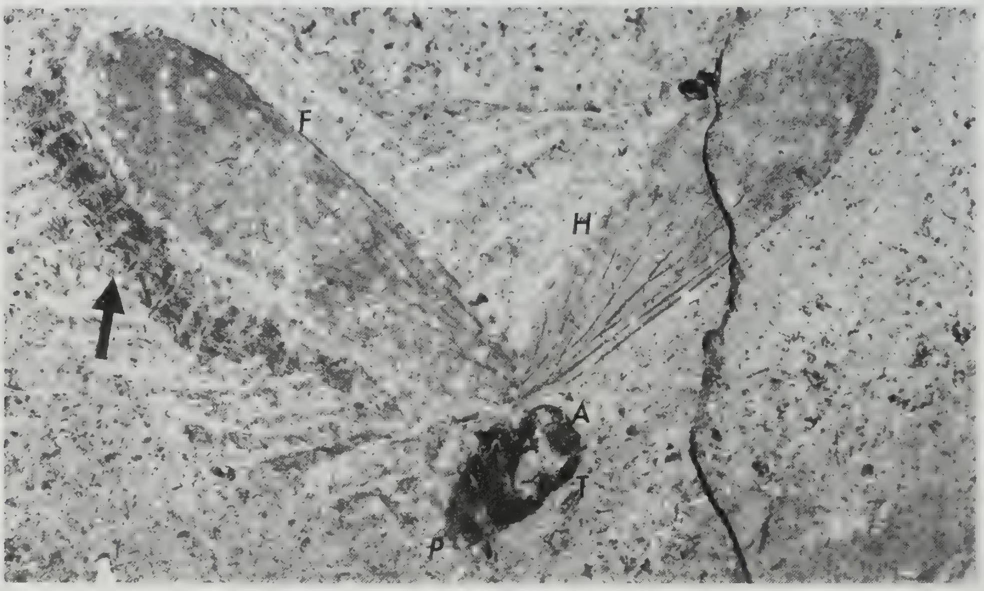


Fig. 47 *Orthophlebia capillata* sp. nov. (Mecoptera). **Holotype,** In.53924, part. A = anterior of thorax, P = posterior of thorax, F = forewing, H = hindwing, T = thorax. Arrow indicates chisel marks, not abdomen. See Figs 48, 51.

The classification of fossil Mecoptera is based mainly on small venational differences. These differences are used at both the specific and generic level but unfortunately we do not know how much intraspecific variation there is in these characters. Some of the finer points, such as the minor branching of veins near the wing margin, may well prove to be intraspecific. There are 15 specimens in the Jackson collection although several are represented by only small fragments. Three species are recognized.

Suborder **EUMECOPTERA**

Family **ORTHOPHLEBIIDAE** Handlirsch, 1906

Diagnosis. Forewing with long subcostal vein reaching the pterostigma. Radial vein diverging from Sc with five or seven branches. Usually five medial veins.

This family is known from the Triassic to the Jurassic in Europe, Asia and Australia.

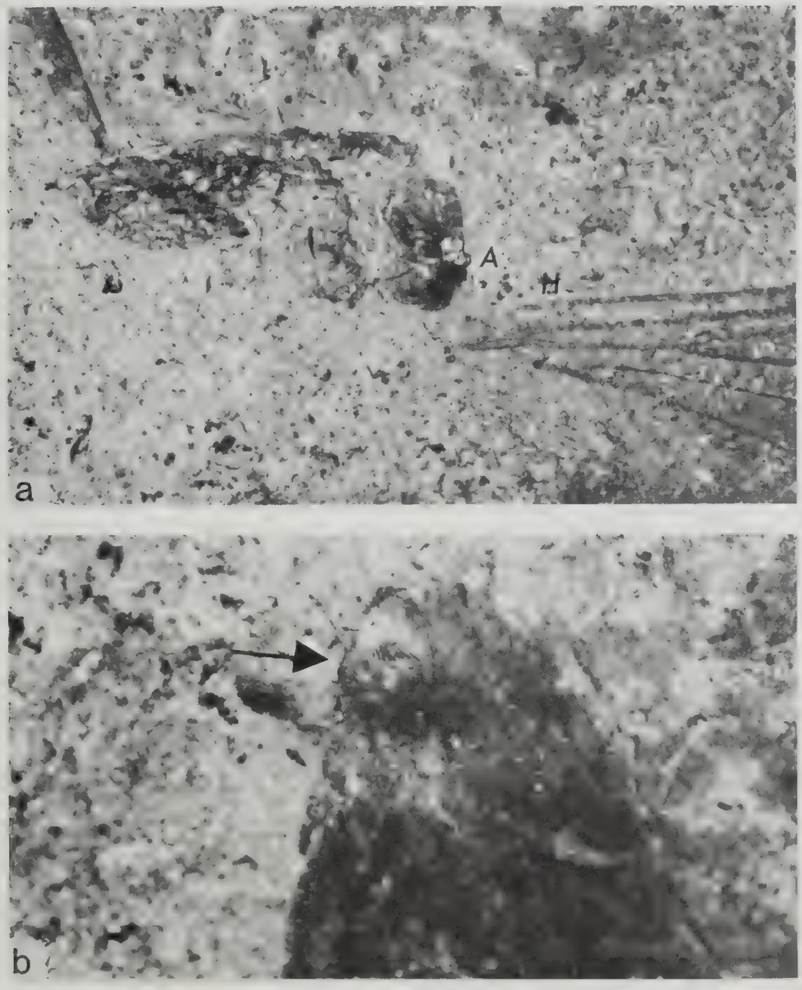


Fig. 48 *Orthophlebia capillata* sp. nov. (Mecoptera). **Holotype,** In.53924, counterpart. a, thorax, 7·5 mm long. A = anterior margin of thorax, H = hindwing base. b, posterior part of thorax to show setae (arrowed). See Figs 47, 51.

Genus ***ORTHOPHLEBIA*** Westwood, 1845

TYPE SPECIES. *Orthophlebia communis* Westwood (*in* Brodie 1845: 102), by subsequent designation of Tillyard, 1933. Upper Triassic and Jurassic of Europe and Asia.

DIAGNOSIS. Orthophlebiids with six or seven branches to Rs.

Orthophlebia capillata sp. nov.

Figs 47–49, 51

DIAGNOSIS. Large orthophlebid with curved Cu_1 in forewing joining Cu_2. Hindwing with Cu_1 and M joined. Veins of hindwing with Y-shaped 1A.

NAME. 'Hairy'.

DESCRIPTION. Forewing, Sc reaches pterostigma; R_1 branches in pterostigma; Rs gives rise to seven final branches on wing margin. Anterior median vein has short branch near wing margin ($M_1 + M_2$) and a single M_3. M_4 and M_5 arise from a short postmedial vein. Cubital vein divides near base into curved anterior and straighter posterior branches. Three anal veins. Few cross-veins preserved. Whole wing covered with microtrichia with larger hairs along veins. Hindwing with humeral vein; seven-branched Rs. M with four branches and Cu_1 arising from near base of M. One cross-vein from CuP to 1A forms part of the distinctive Y-vein formed by 2A. Thorax partially preserved, with clear indication of setae (Fig. 48b), particularly eight post-dorsal setae on metanotum. Prothorax shorter than broad. Part of hind leg, femur 5 mm long, covered with short hairs.

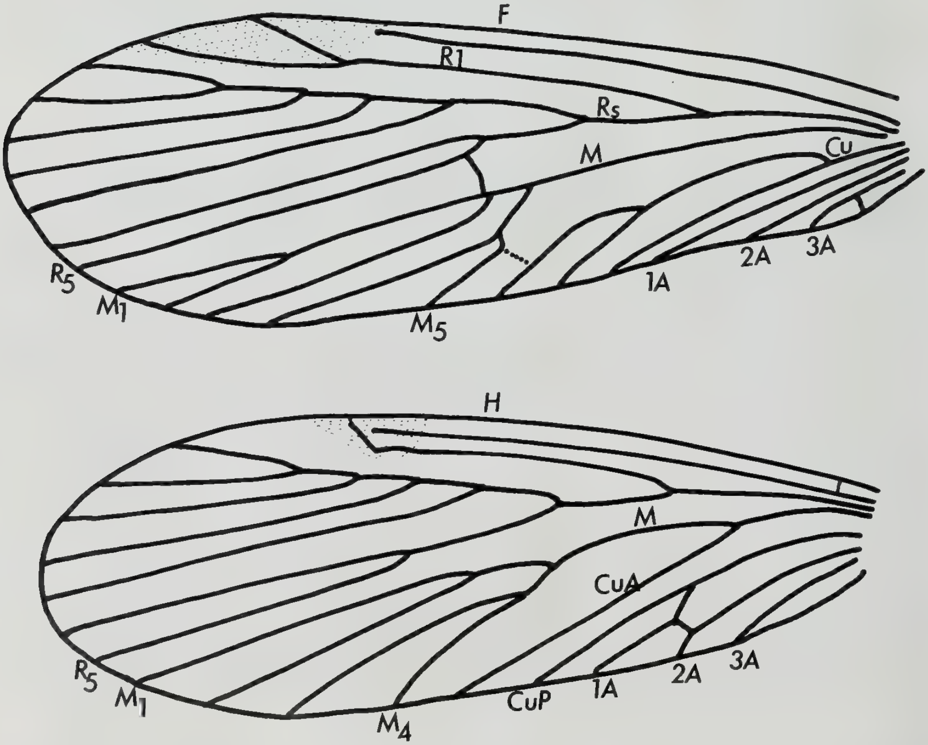


Fig. 49 *Orthophlebia capillata* sp. nov. (Mecoptera). Diagram of wing venations; F—forewing, H—hindwing. A = anal veins, Cu = cubital veins, M = median veins, R = radial veins.

HOLOTYPE. In.53924 (Figs 47–49, 51); Flatstones, Stonebarrow, Dorset; part and counterpart. Jackson colln. Dimensions: Forewing length 24 mm, width 6·3 mm. Hindwing, 21·5 × 6 mm.

PARATYPES. In.49579, In.49601, In.53899, In.59380.

DISCUSSION. The new species from Dorset, with a wingspan of 50 mm, is larger than any other species of *Orthophlebia* except the huge *O. grandis* Martynov 1927, from Turkestan, which has a wingspan of 70 mm. Even *O. gigantea* Tillyard, from the Trias of Strensham (U.K.), had a wingspan of only 38 mm and most Liassic species were much smaller.

All the specimens of *O. capillata* show the very hairy nature of the wings, with hairs on the membrane as well as along the veins. In.53899 shows the microtrichia particularly well when the rock surface is wet; some larger hairs are preserved on the membrane while even larger setal bases are clearly visible along the anal veins: presumably there were originally long setae on these veins. The costal margin is covered with short stout hairs, while the pterostigma is covered by a dense patch of microtrichia. The wing membrane as preserved in some specimens looks as though it may have been slightly thickened and perhaps translucent in life.

The smaller *O. anglicus* described from the Lower Lias of Gloucestershire lacks the Y-shaped second anal vein present in the hindwing of *O. capillata*.

Genus ***PROTORTHOPHLEBIA*** Tillyard, 1933

TYPE SPECIES. *Protorthophlebia latipennis* Tillyard (1933: 28), by original designation. Upper Trias to Upper Jurassic, Europe and Asia.

DIAGNOSIS. Orthophlebiids with a wing length of less than 10 mm. Rs five-branched.

Protorthophlebia latipennis Tillyard, 1933

Figs 50, 52–53

1933 *Protorthophlebia latipennis* Tillyard: 29, fig. 6.

DIAGNOSIS. As genus. Three anteradial veins; setal bases on anal veins large and prominent.

DESCRIPTION. Sc and R_1 end at pterostigma. R_2 forked near wing margin. Two-branched MA, three-branched MP. Three anal veins; CuA curved joining CuP near base. Long hairs on Sc, R, and M at the base, large setal bases on anal veins. Whole membrane covered with short, fine hairs with short, stout hairs along costal margin.

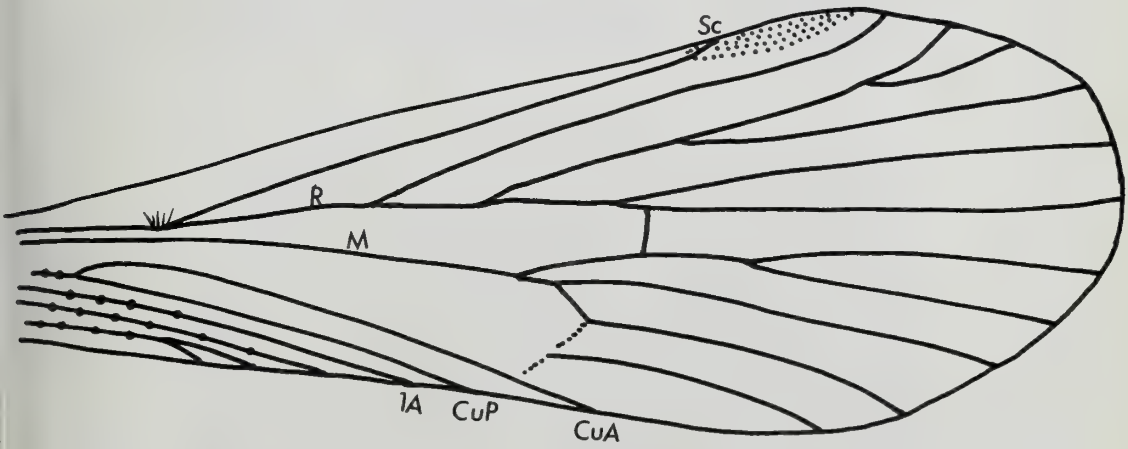
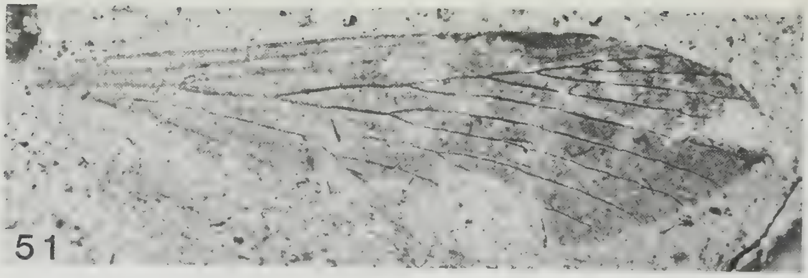


Fig. 50 *Protorthophlebia latipennis* Tillyard (Mecoptera). Diagram of wing venation. A = anal vein, M = median vein, Cu = cubital vein, R = radial veins, Sc = subcostal vein.



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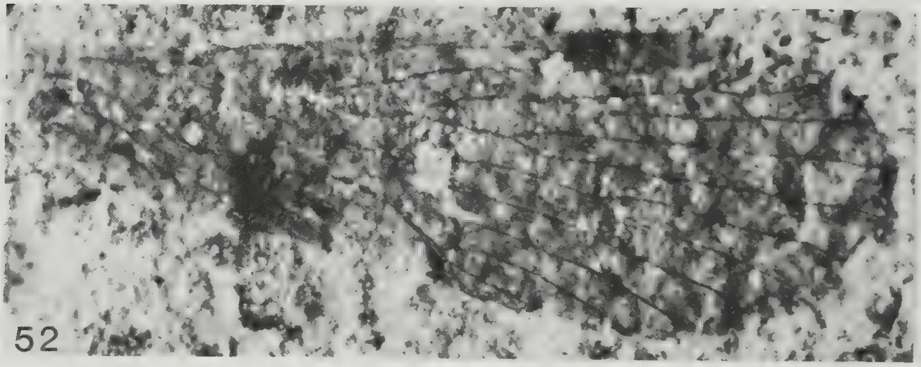

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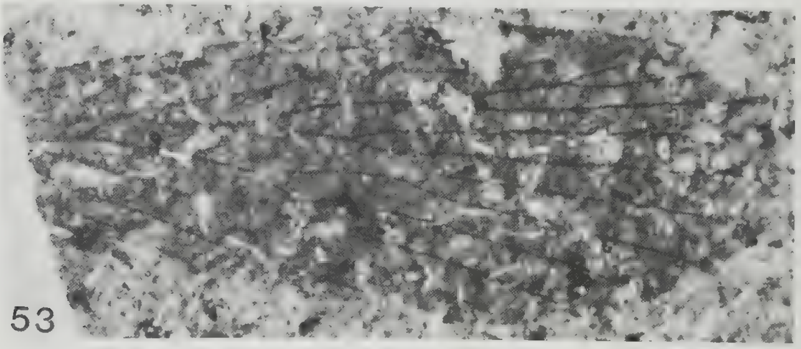

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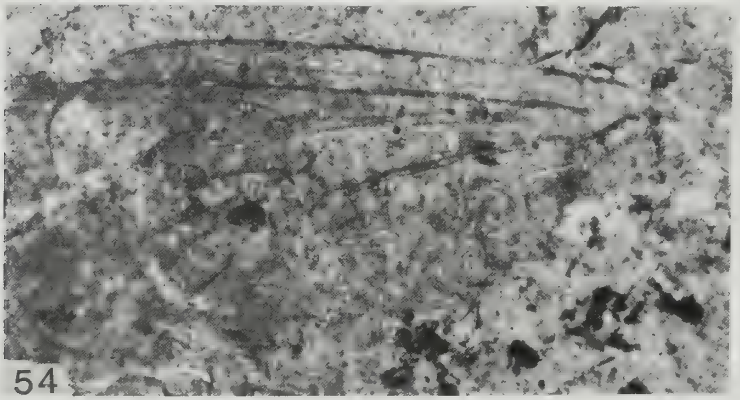

54

Holotype. I.11746; Lower Lias, Binton, Warwickshire. Rev. P. B. Brodie colln., purchased April 1898. Dimensions: Length 9 mm, width 3 mm.

Other material. In.49575, ? In.53954 (Fig. 53), In.53963, In.59120, ? In.59365, In.59371, In.59384 (Fig. 52). Charmouth, Dorset. Jackson colln.

Discussion. Although there are some minor venation differences between the holotype from Warwickshire and the Dorset specimens, most of the venation is very similar. The holotype has a forked vein at the apex of M_1 while this is a single vein in the specimens from Dorset. The holotype is slightly broader in proportion to its length than the Dorset specimens, but is spread out on fine-grain rock while the Dorset rock is coarser and many of the wings are slightly folded: see below. This would certainly be enough to account for the small differences between the specimens.

There is also a stratigraphical difference between the Dorset and the Warwickshire specimens; the holotype is from the older Planorbis Zone of the Lower Lias, while the Dorset material is from the Obtusum Zone.

The presence of a thyridium, represented by the less sclerotized parts of the veins, is indicated by less clearly defined veins at the base of the primary fork of the median vein; it was presumably a flexion line. The large setal bases on the anal veins of the forewing would have had stout setae on them in life, the wings were covered in hairs, and the whole insect probably looked broadly similar to Recent Trichoptera. The strongly curved anterior cubital joining the postcubital near the base is diagnostic of this species. Few cross-veins are preserved, although r-m is clear in one specimen. Specimen In.59120 is slightly damaged and the median veins near the wing margin are not as clear as in others; only four median branches can be traced, although the fifth can just be discerned. In.53954 (Fig. 53) is a slightly larger specimen than the others and is only provisionally placed here.

Family **PSEUDOPOLYCENTROPODIDAE** Handlirsch, 1906

This family formed part of the Paratrichoptera according to Martynov (1927), Tillyard (1935) and Rohdendorf (1962, 1974), but the Paratrichoptera are now considered an early specialization nearer, but not in, the stem-group of the Diptera (Hennig 1981), while the Pseudopolycentropodidae are now placed in the Mecoptera (Willmann 1978). The species currently included in the family are from the Upper Lias or Upper Jurassic of continental Europe; none have previously been reported from the Lower Lias.

Genus ***PSEUDOPOLYCENTROPUS*** Handlirsch, 1906

Type species. *Phryganidium perlaeformis* (Geinitz 1884), by monotypy (Handlirsch 1906: 482). Jurassic, Europe.

Diagnosis. Wing broader in apical third. Sc short; R_1 relatively straight. M five-branched.

Pseudopolycentropus prolatipennis sp. nov.

Figs 55–56

Diagnosis. As genus. Median cell distinct.

Name. *Pro* + *latipennis* (an existing species).

Description. Wing broadly triangular with oblique outer (terminal) margin. Pterostigma present at apex of R_1, almost reaching to R_2. Rs and R_2 diverge sharply with anterior and

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Fig. 51 *Orthophlebia capillata* sp. nov. (Mecoptera). **Holotype,** In.53924, counterpart, hindwing. See Figs 47, 48.

Figs 52–53 *Protorthophlebia latipennis* Tillyard (Mecoptera). Fig. 52, In.59384, forewing, 9 mm long. Fig. 53, In.53954, forewing provisionally placed in this species.

Fig. 54 *Prodocidia spectra* gen. et sp. nov. (Diptera). **Holotype,** In.49226, wing, 7 mm long.

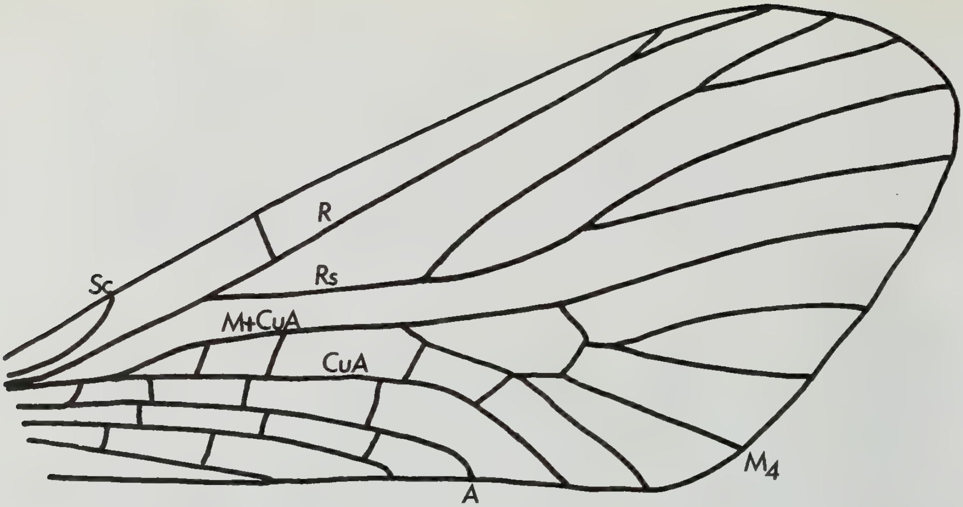


Fig. 55 *Pseudopolycentropus prolatipennis* sp. nov. (Mecoptera). Diagram of forewing venation. A = anal veins, Cu = cubital veins, M = median veins, R = radial veins, Rs = radial sector, Sc = subcostal vein.

posterior branches of R_2 and R_3 curved. Posterior branch from Rs into R_4 and R_5. Five median veins, stem of M curved at base, joining Cu for a short distance before separating median cell formed by anterior and posterior of median vein with M_2 and M_3 on a common stalk. Cu separated from base of M by slightly curved, oblique vein. CuP absent. Three anal veins, unbranched. Single cross-vein visible in costal area just before middle, other cross-veins not visible (? absent) except for anal and cubito-anal areas where they are well developed. Wing veins and membrane hairy with large setal bases along anal veins.

HOLOTYPE. In.53915 (Fig. 56); Woodstones, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 6·3 × 3 mm.

DISCUSSION. *P. prolatipennis* at 6·3 mm long is smaller than *P. latipennis* (8 mm), and has more cross-veins in the anal area. However, the cross-veins are extremely difficult to see and this may be a preservational difference. *P. latipennis* Martynov was found in the Upper Jurassic of Karatau and is similar in shape to the Dorset specimen; both species have the same curious fusion of the median with the cubital vein for a short distance near the base. The membrane of *P. prolatipennis* has preserved very darkly on the rock and may well have been opaque in life.

The family Pseudopolycentropodidae is a curious group with a strongly reduced subcostal vein and the basal vein fusions already mentioned. Martynov (1927: 665) regarded the family as closely allied to the Diptera, 'representing a side-stem, which arose, together with the Diptera, from some unknown Mecopteran ancestor of small size'. The number of anal veins in the suborder Paratrichoptera, to which *P. latipennis* was attributed by Rohdendorf (1962), was regarded as characteristic of the suborder and was given as one or two (1962: 292). This was based on the way the veins join near the base of the wing and assumed that, while the median vein went directly to the base of the wing after joining the cubital, the latter continued along the cross-vein and then ran to the base of the wing. This meant that the rest of the vein was part of the cubital system and was regarded as a postcubital. However, if this latter vein ('CuP') is considered the first anal, then CuP is actually absent. Evidence to support the absence of CuP is shown by the presence of similar small setal bases on each of the 'three' anal veins, whereas these types of setal bases are absent from the anterior cubital vein. It is unusual for the cubital to join with the first anal vein, but not impossible.

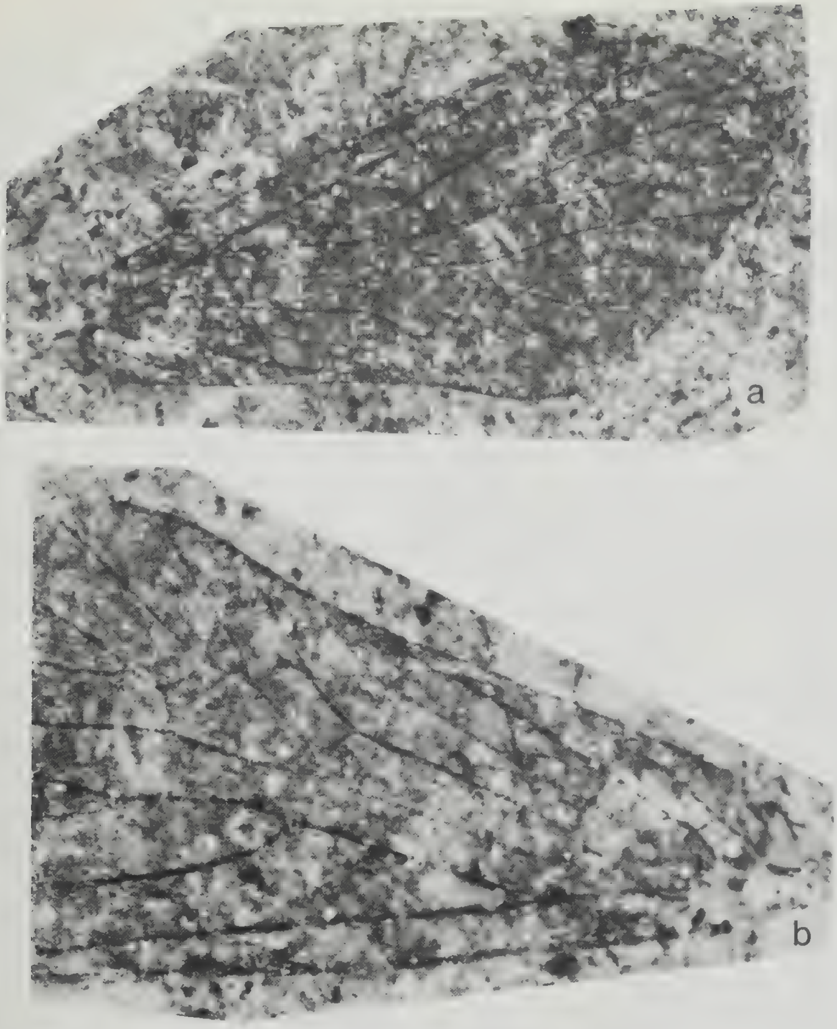


Fig. 56 *Pseudopolycentropus prolatipennis* sp. nov. (Mecoptera). **Holotype,** In.53915. a, part, forewing, 6·3 mm long. b, counterpart, basal area of wing.

The exact interpretation of these veins will have to await discovery of more specimens in this and related genera. Certainly the wing is highly specialized, with the reduced subcostal vein forming a small 'costal brace' and a distinct strengthening of the wing by the formation of the medial cell to take account of the changed shape of the wing. *P. prolatipennis* can be regarded as a highly specialized Mecopteran and unlikely to have been the direct ancestor of any modern order. However, it does show various wing modifications and venation specializations indicating how the development of the modern Diptera–Lepidoptera types may have evolved. The fossil record of the Pseudopolycentropodidae suggests that the group was widespread across Europe and Asia in the Mesozoic.

Order **DIPTERA**, two-winged flies

Only a single wing in the Jackson collection is clearly dipterous, although one other, possibly dipterous, was found closely associated with an ammonite and a species of Raphidioptera (p.

148; Fig. 45). Diptera are rare in the early Jurassic (Rohdendorf 1974, Kovalev 1982) and any specimen which can be recognized, even if only to the Order Diptera, deserves a detailed analysis. The Lower Lias specimen is damaged at the wing apex and part of this is torn and folded over. The posterior wing margin is indistinct and Fig. 57 shows the extent of the visible wing membrane; this is probably reasonably near the actual wing margin. There is a series of brown veins, mostly with fine hairs, as well as raised veins or folds in the wing which are not coloured. The wing has a straight radial vein (R_1) and the radial sector and median veins run close together and are virtually inseparable for part of their length. It is possible that the wing membrane may be slightly folded which would account for the approximation of the radial sector and median veins. The cubital vein is thick and double with the postcubital not reaching the wing margin. The anal area was probably relatively large, judged from the extent of the preserved wing membrane, but only one anal vein is present.

Suborder **NEMATOCERA**

Superfamily **BIBIONOMORPHA**

Family **MYCETOPHILIDAE** Macquart, 1838

The new genus described below is only provisionally placed in this family. Whilst it broadly resembles Recent *Diadocidia* Ruthe (which is sometimes placed in its own family, Diadocidiidae), the larger family Mycetophilidae *sens. lat.* is preferred. The fossil species is placed within the broad division of fungus-gnats (Fungivoridea, auctt.) and probably should be placed in a family of its own.

Genus ***PRODOCIDIA*** gen. nov.

Type species. *Prodocidia spectra* sp. nov. Lower Lias, U.K.

Diagnosis. Sc long, reaching almost to apex of wing. Pterostigma present. Rs and M run close together. Cell elongate. The long subcostal vein separates this genus from the rest of the Fungivoridea of Rohdendorf.

Name. Greek *προ* + *δοκίδιον*, a small shaft.

Prodocidia spectra sp. nov.

Figs 54, 57

Diagnosis. As genus.

Name. 'Images in the mind'.

Description. Apex of wing damaged; exact extent of all wing margin indeterminate but dotted line in Fig. 57 shows extent of preserved membrane. A broad wing, humeral vein near base of subcosta. R_1 simple, Rs arises towards base of wing and runs close to M. Probably two apical branches to Rs. M with two apical branches, m-cu cross-vein distinct, forming part of elongate cell. Cubital cell double along hind margin of cell, Cu_1 continues to wing margin. Strongly curved, single, anal vein. Costal vein with fine hairs, macrotrichia on wing base.

Holotype. In.49226 (Fig. 54); Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Length 7 mm.

Discussion. The length of the subcostal vein, almost reaching the wing apex, distinguishes this species from most fossil fungus-gnats (Fungivoridea, auctt.) and also from Recent species of *Diadocidia*. Apart from the length of the subcostal, the rest of the venation is similar to a group of Recent genera of fungus-gnats, including *Diadocidia*, *Symmerus* Walker and *Ditomyia* Winnertz (McAlpine *et al.* 1981). The cell in *P. spectra* is well marked and elongate, and the pterostigma is marked by numerous microtrichia. Fungus-gnats have been recorded from the Triassic and Jurassic rocks of the U.S.S.R. (Rohdendorf 1962) and are widespread and abundant at the present day.

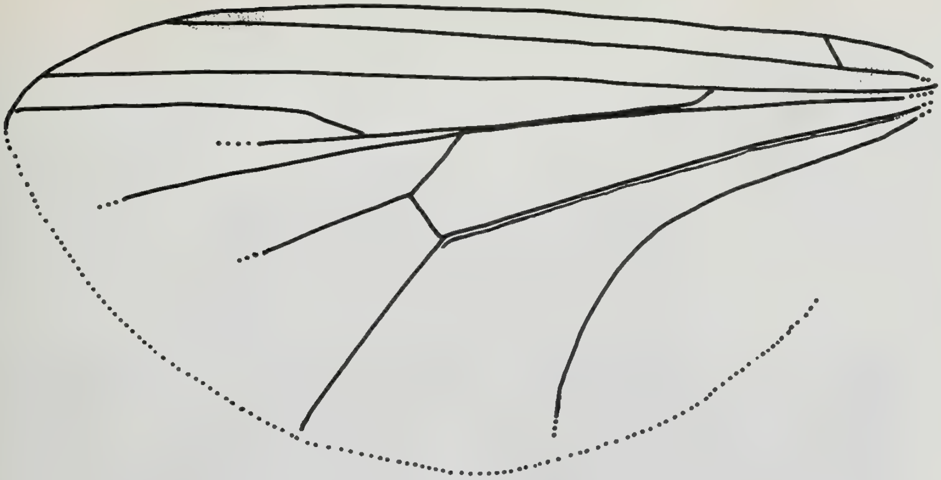


Fig. 57 *Prodocidia spectra* gen. et sp. nov. (Diptera). Diagram of wing venation.

Order **LEPIDOPTERA**, butterflies and moths

When a piece of Dorset Lias, collected by Jackson, was recently split it revealed a small scale-covered wing. This discovery has significance in the continuing debate on the evolution of the Lepidoptera, to which the fossil is attributed. There is no other direct evidence of scale-covered wings earlier than the Upper Jurassic, 40–50 million years later (Rasnitsyn 1983). It is important, therefore, to give careful consideration to the systematic position of this fossil.

The earliest recognized scale-covered wings of Lepidoptera are from the Upper Jurassic (Rasnitsyn 1983) and the Lower Cretaceous, where a moth was found in Lebanese amber (Whalley 1978). Other, unassociated, scales were also found in this amber; on the basis of the specimen and the isolated scales two families of Lepidoptera, Micropterigidae and Incurvariidae, were recognized. Riek (1976) and Tindale (1980) described wings they consider lepidopterous from the Upper and Middle Trias respectively but these do not have any preserved scales.

Although scales are characteristic of Lepidoptera, they are not exclusive to them and are also found in the Psocoptera, Diptera, Coleoptera and Trichoptera amongst the winged insects. From a study of these groups only the Amphiesmenoptera (Lepidoptera + Trichoptera and their stem-group; Kristensen 1975) are considered to have characters that occur in the fossil wing.

Family **ARCHAEOLEPIDAE** nov.

Diagnosis. Scale-covered wing with prominent forked cubital vein. Vein R_1 forked at apex. Scales with longitudinal ridges and few cross-ribs (trabeculae, Imms 1970). Radial vein four-branched; median three-branched.

Discussion. The family is separated from the Micropterigidae by the wing venation, particularly the anal veins. At present known from one wing, probably a hind wing. Lower Lias, U.K.

Genus ***ARCHAEOLEPIS*** nov.

Type species. *Archaeolepis mane* sp. nov.

Diagnosis. As family. Subcostal vein probably simple, 1A and 2A probably joined.

Name. 'Ancient scale'.

Archaeolepis mane sp. nov.
Figs 58–60

DIAGNOSIS. As family.

NAME. 'Dawn'.

DESCRIPTION. Heavily scaled (? hind) wing. R_1 forked at apex, Rs forked, probably with third fork though origins obscure. Three median veins, obscure towards base. Cu clearly divided. 1A and 2A probably join; tip of 3A and rest of anal area indistinct. Scales 0·20–0·23 mm long, 0·06–0·08 mm wide. Strongly ridged, ridges vary in width, according to the width of scale, usually 0·002 mm apart. Cross-ribs mostly absent, although some lateral connections between

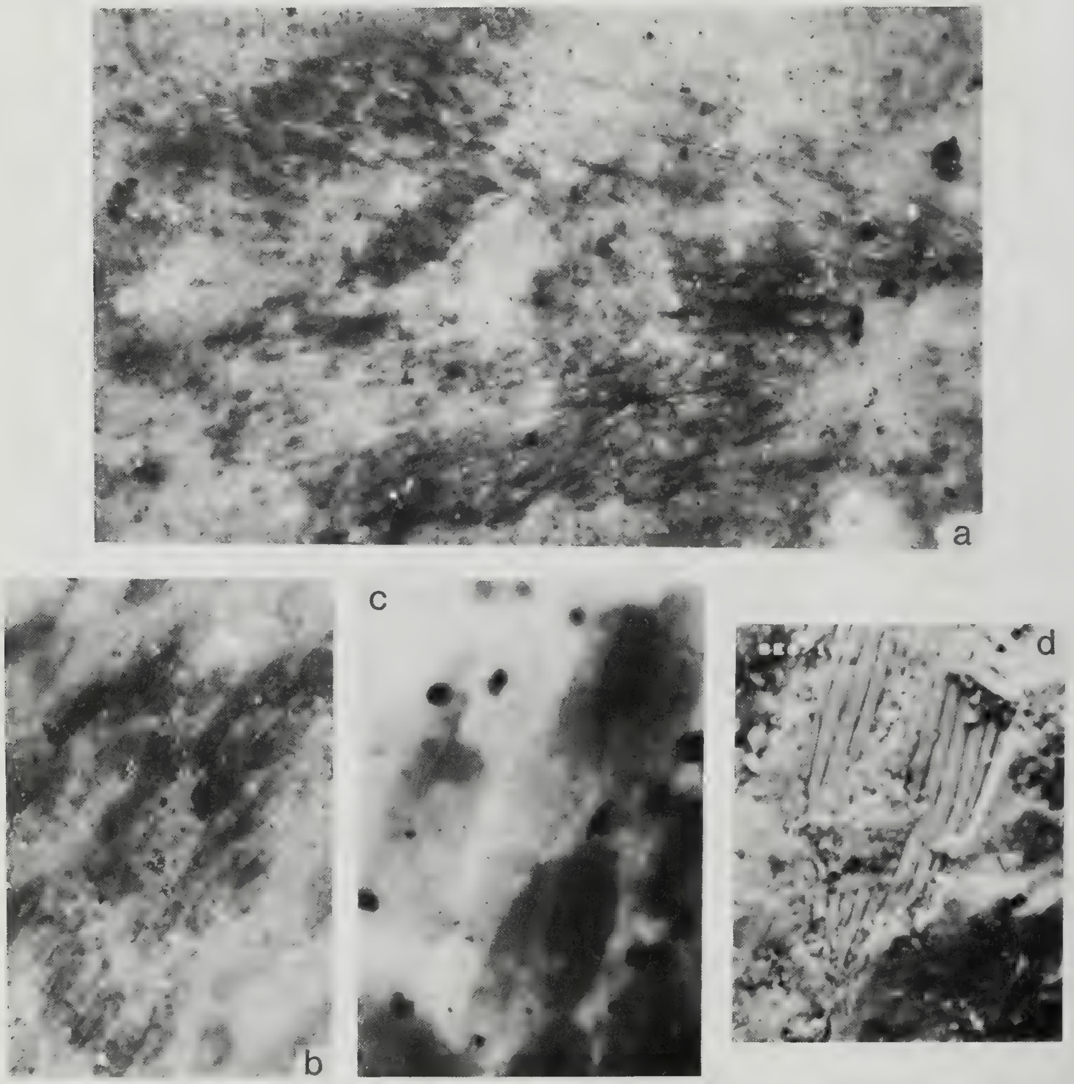


Fig. 58 *Archaeolepis mane* gen. et sp. nov. (Lepidoptera). **Holotype,** In.59397. a, wing, 5·3 mm long. b, wing scales, length of scales 0·20–0·23 mm. c, wing scales under ultra-violet light. d, stereoscan micrograph of uncoated wing surface, showing scales; magnification *c.* × 2000.

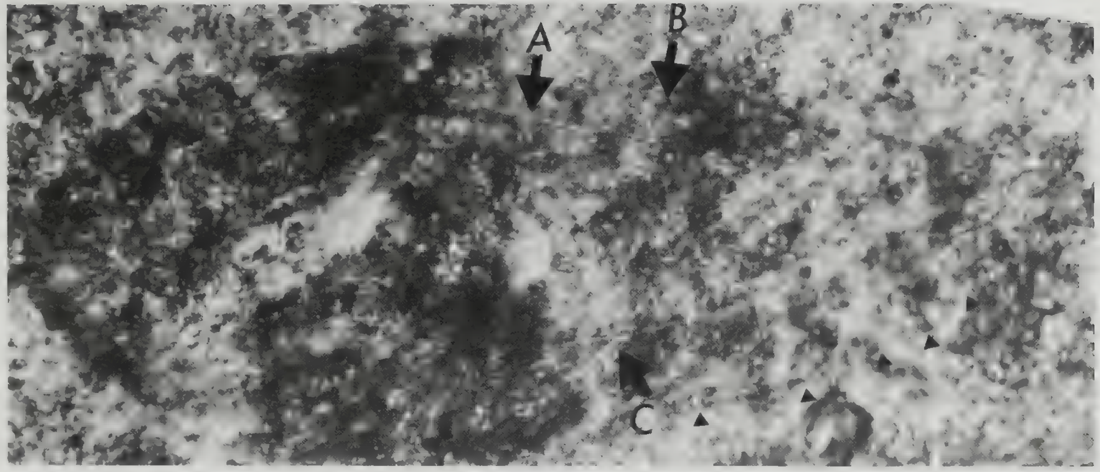


Fig. 59 *Archaeolepis mane* gen. et sp. nov. (Lepidoptera). Holotype, In.59397, whole wing under ultra-violet light. A = radial vein, B = subcostal vein, C = cubital fork. Small arrowheads indicate extent of hind margin of wing in anal area.

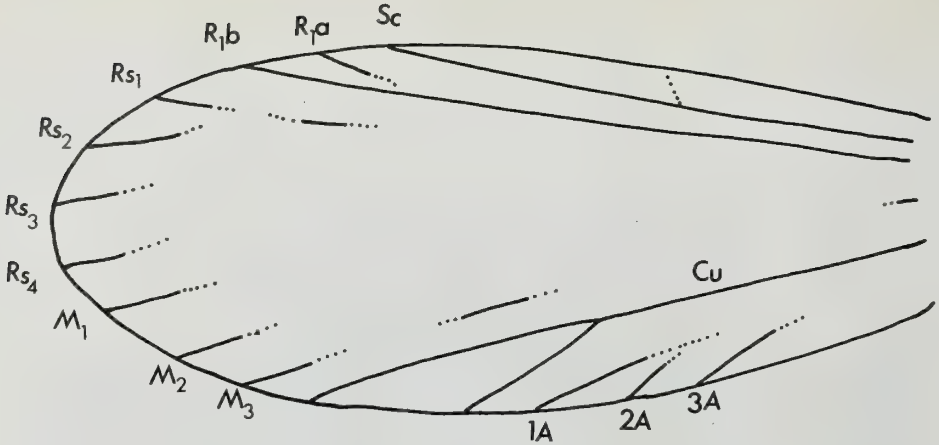


Fig. 60 *Archaeolepis mane* gen. et sp. nov. (Lepidoptera). Composite diagram of wing venation. A = anal veins, Cu = cubital vein, M = median veins, R = radial vein, Rs = branches of radial sector, Sc = subcostal vein.

the longitudinal ridges are apparent near base of some scales. Apex of scales smoothly rounded. Two, possibly more, different types of scales. Marginal scales thinner, some thinner scales mixed in with thicker ones on wing membrane. The wing margin has longer scales along the hind margin and probably had a substantial fringe of scales. Fewer ridges on some scales, 12–13 as against 18–22 on others. The ridges on the scales as seen in the stereoscan micrographs (Fig. 58d) are considered to represent the infilling between the original ridges (striae) and their compression, with the dark lines representing the ridges from the original scale. The scales shown in the micrographs are the narrow ones with fewer striae.

HOLOTYPE. In.59397 (Figs 58–59); Birchi nodules, Lower Lias, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: Length 5·3–5·6 mm, width 2 mm.

DISCUSSION. Although Lepidoptera or Trichoptera are the most obvious orders for the fossil wing, others cannot be eliminated without further consideration. Indeed some of the Recent scaly-winged Lepidopsocidae (Psocoptera) look superficially very similar to the Dorset fossil. Apart from these, consideration was also given to the possibility that the wing represented an extinct, scale-winged mecopteran (*sens. lat.*). Several families in the broad assemblage Mecopteroidea (Willmann 1978) have been considered as giving rise to the modern Diptera, Trichoptera and Lepidoptera (Tillyard 1933). Many Jurassic Orthophlebiidae have an unbranched cubital vein, contrasting with *Archaeolepis*, and are really early Mecoptera. The Pseudopolycentropodidae, which have a highly specialized and slightly lepidopterous wing shape, are also still considered Mecoptera (Willmann 1978). All these are known from the same deposit as *Archaeolepis*. Many of the fossil orthophlebiids from the Jurassic have the hairs clearly preserved on the wings but none are known with vein M_4 absent (as in the fossil). Although the Order Mecoptera was more diverse in the Mesozoic there are no living representatives with scale-covered wings, as there are for the other orders discussed below.

PSOCOPTERA. This order is known from the Permian and there are two Recent families, the Amphientomidae and Lepidopsocidae, which have completely scale-covered wings (Enderlein 1906). The psocid wing differs from *Archaeolepis* in venation, with Sc and R not running parallel and Cu unbranched. Some of the scales are toothed at the apex but the underside differs from lepidopterous-type scale with thickened ridges running transversely across the scale. In some of the fossil species of *Permopsocus* Tillyard, Cu is forked but Sc and R do not run parallel as in *Archaeolepis*. Thus the fossil *Archaeolepis* can be ruled out of the Psocoptera.

DIPTERA. Scales are present on the wing of many nematoceran Diptera and in the Psychodidae the wings are completely clothed with hairs and scales. In most Diptera, the scales, when present, are restricted to the veins although in the Cecidomyiidae the scales may cover the wings. In *Psychoda surcoufi* Tonnoir the wing is covered with long hair-like scales which are elongate and have a distinctly serrate edge, very similar to the elongate hairs of the Trichoptera. The scales in *Archaeolepis* are larger and their arrangement on the wing is different from Diptera of comparable size. Comparisons have been made with the scales of Recent mosquitoes, which are broadly similar but the venation and anal area are different. The scales on most mosquitoes are arranged along the veins. The fossil wing is not considered dipterous.

TRICHOPTERA. While the majority of Recent species have hairy wings, most of the families of the Suborder Integripalpia have a few species where the wings are covered in scales. These scales vary in shape and size and when studied under the stereoscan electron microscope cross-ribs can be seen. In the sister-group of the Integripalpia, the Suborder Annulipalpia, the wings are hairy and scales are not developed. Hennig (1981) commented that it is virtually impossible to separate the Lepidoptera and Trichoptera on wing venation alone. Probably the only apomorphic character in the wings of Lepidoptera is the fusion of M_4 with CuA, leaving, in effect, only three medial veins, as shown by *Archaeolepis*. Kristensen (1984) points out that M_4 is present in the fore (and some hind) wings of Lepidoptera Aglossata. While the scales on the wings of some Trichoptera are quite dense, they are frequently smaller than in Lepidoptera and do not usually give the overlapping cover typical of Lepidoptera.

LEPIDOPTERA. Although other lepidopterous groups, such as the Heterobathmiina, have been considered, the comparison of *Archaeolepis* is better made with the more primitive group Micropterigidae (Kristensen 1979) and more especially with species of *Sabatinca* Walker. A complete scale-covering of the wing is typical of the Micropterigidae and is similar to *Archaeolepis*. The shape and such venation as is preserved in the fossil is mostly consistent with the hind wings of Micropterigidae, and this, together with the forked cubital vein, is not inconsistent with the stem-group Amphiesmenoptera. Under the stereoscan the scales of *Archaeolepis* show a virtual absence of cross-ribs, a condition similar to the Micropterigidae and Eriocraniidae (Kristensen 1970). The subcostal vein in the fossil may be simple, the base is not clear and the radial fork (R_1a, R_1b) is similar to species of *Sabatinca*. The exact number of median veins in *Archaeolepis* is difficult to determine but there are probably three branches as in the Micropterigidae. If lepidopterous, then *Archaeolepis* is either the sister-group of the Zeugloptera (Micropterigidae) or of the Zeugloptera + Glossata + Heterobathmiina + Aglossata. Without further data neither this, nor even the position of *Archaeolepis* within the Lepidoptera itself, can be resolved.

In a recent paper Rasnitsyn (1983) reported traces of scales on a small insect from the Upper Jurassic of the U.S.S.R. He proposed a new suborder of Lepidoptera (Eolepidopterigina) and new family (Eolepidopterigidae) for the specimen, which he described as *Eolepidopterix jurassica*. No apomorphic characters were indicated to confirm the lepidopterous nature of the specimen nor did he say how it differed from scaly-winged Trichoptera. For the present I do not propose to place my new family, Archaeolepidae, in his new suborder but I certainly regard his evidence as showing that *Eolepidopterix* is lepidopterous.

Archaeolepis extends the age of these scale-winged insects back a further 45–50 million years, and new origins will have to be sought for the Lepidoptera in the Upper Triassic, as suggested by Riek (1976), or even the Middle Triassic (Tindale 1980). Probably the most important implication of *Archaeolepis* is not so much in the overall picture of the antiquity and evolution of the Lepidoptera, but in the Lepidoptera–plant relationship. Currently Lepidoptera are considered to have arisen at about the time of the earliest angiosperm (i.e. Upper Jurassic–Lower Cretaceous; Hughes 1976), and to have paralleled their evolutionary diversification. The latter is certainly true but it now appears that the scale-winged insects arose well before the earliest angiosperm. There is, however, no need to link the earliest Lepidoptera with angiosperms because many Recent lepidopterous larvae are capable of feeding on a wide range of non-angiospermous plants. This fact, however, is not proof that their ancestors did, since it might be a secondary habit. The existence of *Archaeolepis* well before the earliest angiosperm is more convincing evidence that early lepidopterous larvae probably did *not* feed on angiosperms. There were undoubtedly sources of pollen or spores for the adult food, as used by adult moths in the Recent Micropterigidae. Sources of liquid food, extra-floral nectaries, plant exudates etc., were available before the angiosperms and although the development of a lepidopteran-type proboscis cannot be entirely ruled out there is no evidence for its development in the Lower Jurassic. An analogy is therefore drawn between the pollen-feeding habits of modern adult Micropterigidae and the possibility that a similar method was available to *Archaeolepis*.

What is indisputable is that, in the Lower Jurassic, there were small moth-like insects with scale-covered wings. The delicate nature of the *Archaeolepis* wing suggests that it was not transported very far before fossilization, suggesting the site was near to a land mass.

Order **COLEOPTERA**, beetles

Beetles are the most abundant insects in the Dorset Lias, forming over 39% of the total insects found. This not only shows their undoubted abundance in the fauna from which the deposits were derived but also is a reflection of the durability of the toughened beetle elytra. Beetles are usually very strongly sclerotized with the elytra particularly tough in most cases. Up to 40% of the beetle fossils are represented by both elytra (as well as other parts) while in other orders fewer than 10% of the insects are represented by both forewings, even in groups where the forewings are more sclerotized than the hindwings (Orthoptera, Blattodea). For some reason the elytra from a single individual beetle were less likely to be separated than the forewings of other orders.

It is difficult, in many cases impossible, to place a single elytron (or even a pair of elytra) into a modern family reliably. The lack of venation in the elytra, which is used to identify the family in many other orders, is not compensated for by the increased sculpturing; the latter is sometimes a guide to the family but frequently elytral sculpturing is of no use on its own at the family level. Where a single elytron can be associated with a family (usually after consultation with a Coleoptera specialist), this has been given; the remaining unassociated elytra, which are often very distinctly patterned, are associated in species groups. This gives some indication of the diversity of the fauna, since they are associated on shape, size and the sculpturing of the elytra. An estimate of the total number of different species groups is considered to represent an approximation of the number of species of beetles. From this it is estimated that there are not fewer than twenty, and probably at least thirty, distinct species of beetles in the Dorset Lias. Comparison of these 'species' has been made with the beetle faunas described by Ponomarenko (1969) and Arnoldi (1977) from the Mesozoic of the U.S.S.R.

Family **ELATERIDAE** Leach, 1815

Genus ***ELATERINA*** Gardiner, 1961

TYPE SPECIES. *Elaterina liassica* Gardiner, by original designation (Gardiner 1961: 87). Lower Lias, U.K.

Elaterina liassica Gardiner, 1961

This genus and species were based on a single elytron found in the orbit of a fish during acetic acid preparation. The elytron, incomplete and in poor condition, has few details preserved. There is a distinct 'rim' along one side but the striae are barely visible. There is nothing left on the specimen to indicate that it is an elaterid beetle, and its elytra at 12·5 mm are longer than in any other Elateridae from the British Lias. It has not been possible to recognize this species from the many new specimens collected in the same locality but one specimen, In.59369, which has roughly similar dimensions, is provisionally associated with *E. liassica*.

Genus *ELATEROPHANES* Handlirsch, 1906

TYPE SPECIES. *Elater vetustus* Brodie 1845, here designated. Lias, U.K.

DIAGNOSIS. Prothorax about as broad as long, with elongate posterior corners.

DISCUSSION. Handlirsch (1906: 436) proposed *Elaterophanes* for two species, both based on specimens from the Lower Lias of Apperley, Gloucestershire, and illustrated by Brodie (1845: pl. vii, figs 1 & 2). Brodie (1845: 10) named one specimen (pl. vii, fig. 1) as *Elater vetustus* but left the second specimen un-named in the family Elateridae. Giebel (1856) named this second specimen *Elater socius*, and Handlirsch transferred both species to *Elaterophanes* (1906: 436). Examination of both Brodie's original specimens indicates that *E. socius* Giebel should be regarded as a junior synonym of *E. vetustus* Brodie. Dolin (1975) mentioned that the systematic position of *Elaterophanes* had not been elucidated. Examination of the type specimen of *E. vetustus* and a study of Dolin's key to the Elateridae (1975: 475) suggests that this genus would fit in the tribe Hypnomorphini. The femoral plates on the hind coxae do not have an extra long side, as in the Desmatini, and the prosternal suture looks closed along its length.

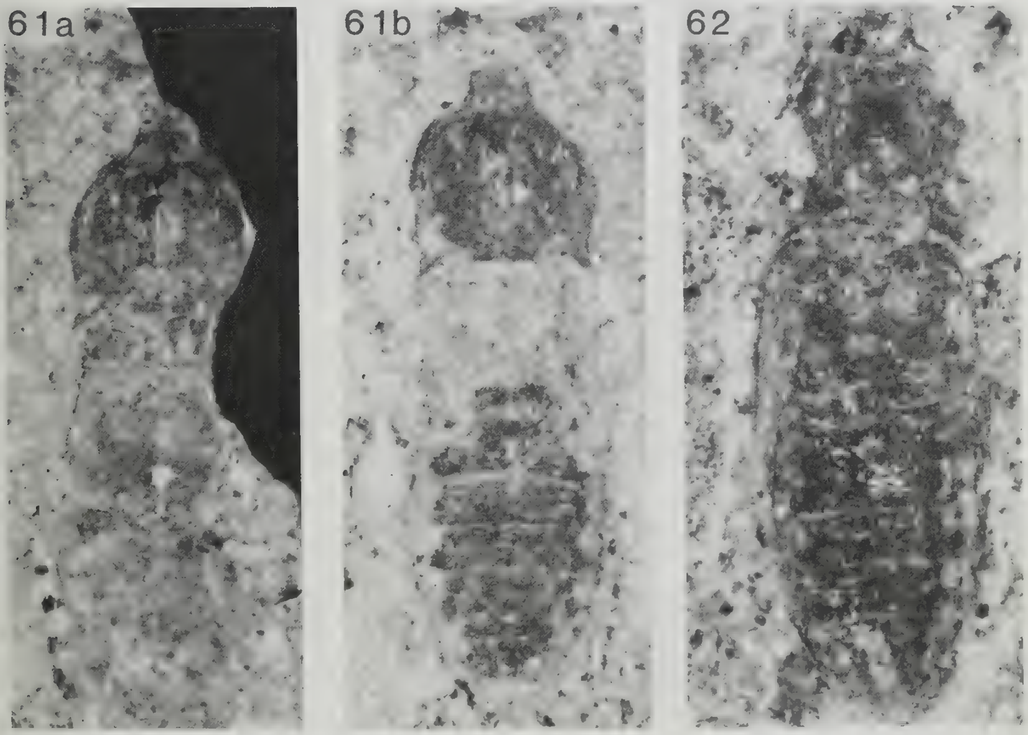
Elaterophanes regius sp. nov.

Figs 61–62

DIAGNOSIS. As genus, but smaller than type species and with lateral thoracic margins curved, not straight.

NAME. 'Kingly'.

DESCRIPTION. Head small in proportion to thorax. Prothorax rounded anteriorly. Elytra not visible. Base of coxae visible; peg-like process at base of prothorax and probable cavity faintly



Figs 61–62 *Elaterophanes regius* sp. nov. (Coleoptera). Fig. 61, **holotype,** In.59385, length 7 mm. a, part. b, counterpart. Fig. 62, paratype, In.53952, length 8 mm.

indicated in anterior (ventral) of mesothorax. These structures form part of the peg click-mechanism of the beetle. Abdomen elongate, slightly broader posteriorly. Apex of abdomen with slight swelling indicating female genitalia.

Holotype. In.59385 (Fig. 61); Flatstones, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 7–8 mm body length.

Paratype. In.53952 (Fig. 62); data as type.

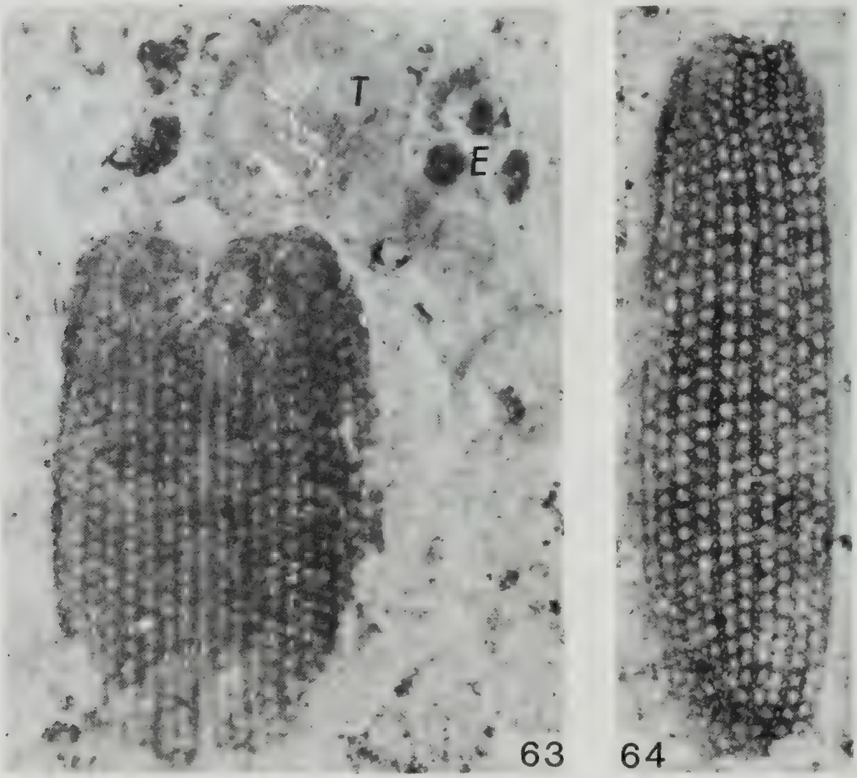
Discussion. The general shape of this click-beetle is very similar to Recent species of *Agriotes* Eschscholtz. *E. regius* is smaller than *E. vetustus* (Brodie) (10 mm long) from the Lower Lias, Gloucestershire. The elytra of *E. regius* are probably buried beneath the visible parts of the fossil. The paratype is the larger specimen but otherwise their preservation and proportions are similar except that the eyes are more clearly preserved on the paratype specimen. *Elaterophanes regius* is provisionally placed in the Hypnomorphini but the main diagnostic characters for this tribe are not clear on the fossil.

Family **CUPEDIDAE** Latreille, 1825

Genus ***LIASSOCUPES*** Zeuner, 1962

Type species. *Liassocupes parvus* Zeuner, by original designation (Zeuner 1962: 167). Lower Lias, U.K.

Diagnosis. Cupedid with rounded pronotum (Zeuner 1962).



Figs 63–64 *Liassocupes parvus* Zeuner (Coleoptera). Fig. 63, holotype, In.64008, elytra 4 mm. E = eye, T = thorax; head and thorax rotated, see p. 167. Fig. 64, In.49210, elytron 4·8 mm long.

Liassocupes parvus Zeuner, 1962
Figs 63–64

1962 *Liassocupes parvus* Zeuner: 167, pl. 27, fig. 4.

In the type specimen the head and thorax, if in fact they are part of the same specimen, are rotated at an angle to, and slightly separated from, the elytra (Fig. 63). The actual shape of the thorax is indistinct; it may well have been longer than broad. One new specimen (In.49210, Fig. 64) from the type locality is regarded as conspecific: it is a single complete elytron which clearly shows the typical cupedid pattern. Its width is the same as the incomplete holotype, but it is longer because it is complete.

HOLOTYPE. In.64008 (Fig. 63); Flatstones, Black Ven, Charmouth, Dorset. Jackson colln. Dimensions: Length (incomplete), 4 mm.

OTHER MATERIAL. In.49210 (Fig. 64); data as holotype. Dimensions: Length (complete), 4·8 mm.

Liassocupes (?) ***maculatus*** sp. nov.
Figs 65–66

DIAGNOSIS. Cupedid with 12 rows of pale spots; whole elytra covered with black spots.

NAME. 'Spotted'.

DESCRIPTION. External margin flattened, broadest towards thorax. Margin clearly with row of paler areas; junction between flattened edge and curved part clearly defined, resembling a subcostal vein. Elytra covered by rounded and equally spaced black spots. Apex of elytra pointed. On counterpart (In.53949, Fig. 66b) the black spots are more concentrated in anterior part. Pale areas slightly broader laterally, clearly demarcated by darker areas between.

HOLOTYPE. In.49577 (Fig. 65); Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Length 12·2 mm, width 3·8 mm.

PARATYPES. In.51038, In.53949 (Fig. 66), In.59133. Same data.

OTHER MATERIAL. In.59361, ? In.59154.

DISCUSSION. This species is only provisionally placed in *Liassocupes*. It has particularly well-marked and distinctive elytra with part and counterpart showing slightly different features. The flattened rim is very sharply demarcated from the curved part and may be marked by a vein; alternatively this appearance may be due to the concentration of black dots along this line. The striae do not show clearly on this species.

Liassocupes (?) ***giganteus*** sp. nov.
Fig. 67

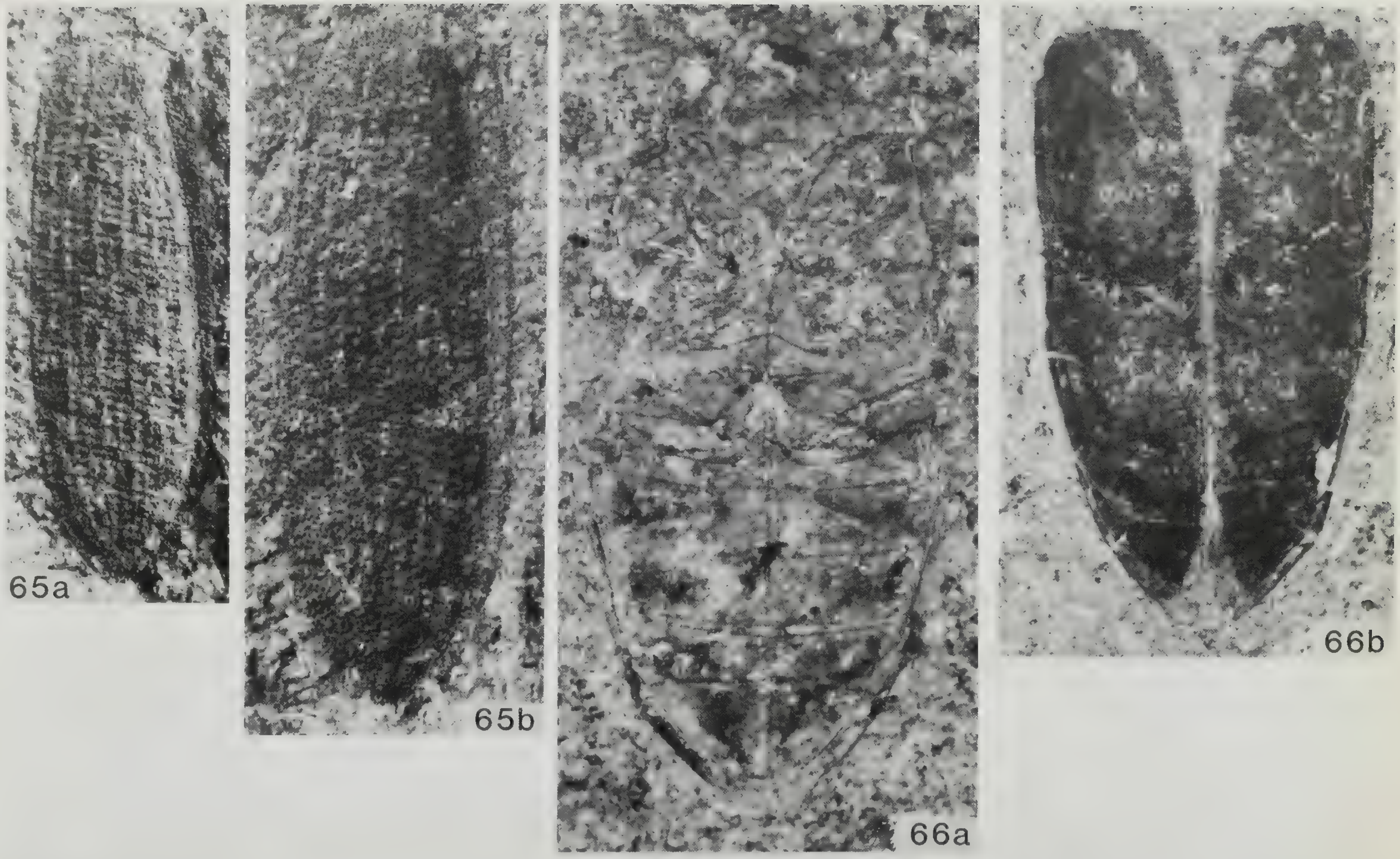
DIAGNOSIS. Elytra with reticulate pattern and scarcely any trace of longitudinal striae.

NAME. 'Giant-like'.

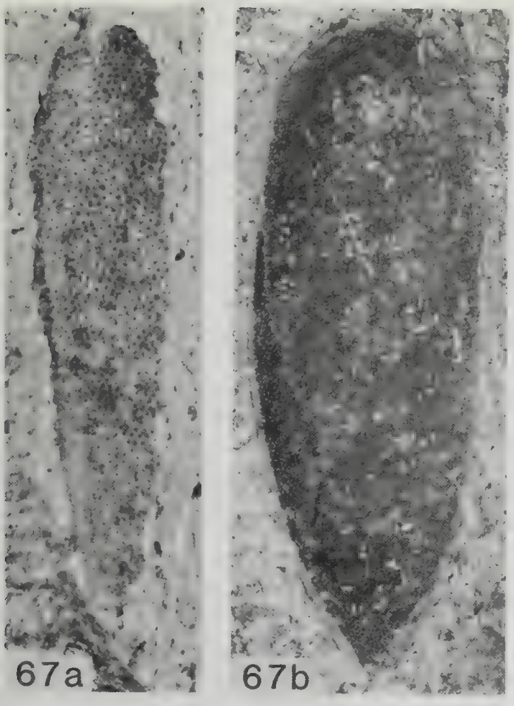
DESCRIPTION. Elytra with pointed apex and rounded anterior margin. Slight lateral flattening along outer margin. Reticulate pattern very distinctive with almost octagonal cells, each with raised central point. Trace of ribbing in subcostal/radial area.

HOLOTYPE. In.51026; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 21·4 × 7·8 mm.

DISCUSSION. This is the largest beetle elytron from the Lias. In several characters it resembles species of Taldycupedidae (Rohdendorf 1962) with similar reticulate pattern and obscure ribbing. At present species of this family are known only from the Permian and Upper Trias. *L. giganteus* is only provisionally placed in *Liassocupes* and might well be a late example of Taldycupedidae.



Figs 65–66 *Liassocupes* (?) *maculatus* sp. nov. (Coleoptera). Fig. 65, **holotype,** In.49577, elytron, 12·2 mm long. a, photographed dry. b, photographed wet. Fig. 66, paratype, In.53949. a, part. b, counterpart: fossil has split between elytra and rest of abdomen.



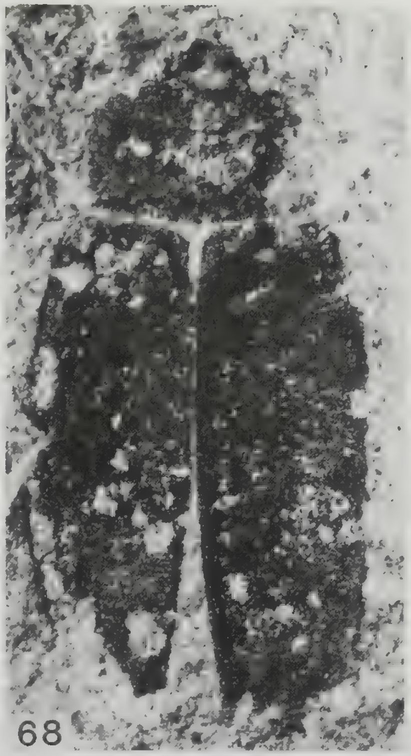


Fig. 67 *Liassocupes* (?) *giganteus* sp. nov. (Coleoptera). **Holotype,** In.51026, 21·4 mm long. a, part. b, counterpart.

Fig. 68 Carabidae (?) species (Coleoptera). In.53923, 11·2 mm long.

Family **CARABIDAE** Latreille, 1825

The following are provisionally placed in this family: In.53923 (Fig. 68); In.51040 (Fig. 69); In.49572 (Fig. 70); In.49222 (Fig. 71).

Superfamily **BYRRHOIDEA**

Provisionally placed in this superfamily: In.64021 (Fig. 72).

Superfamily **DRYOPOIDEA**

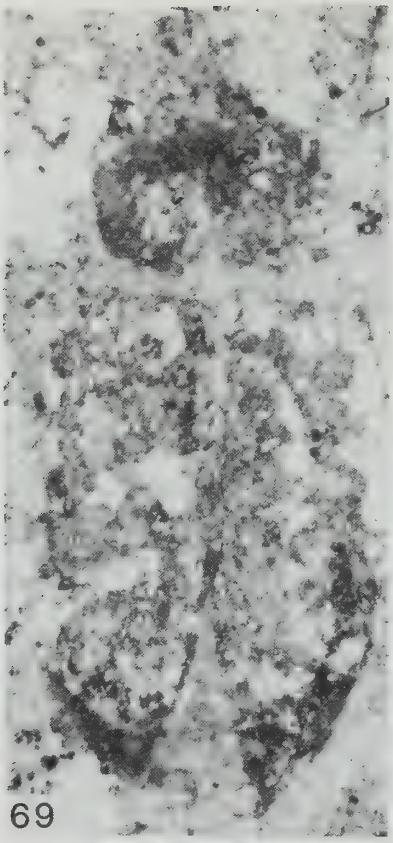
Provisionally placed in this superfamily: In.49215, In.49217, In.49218, In.49562, In.51009 (Fig. 74), In.53896, In.53932, In.53950, In.53992, In.59101 (Fig. 73), In.59122, In.59379, In.59398, In.64024 (Fig. 75). Several of these may be species of Psephenidae; many are probably water beetles.

Superfamily **CURCULIONOIDEA**

Provisionally placed in this superfamily: In.59097, In.64022, In.51000.

Curculionidae, gen. et sp. indet.

One specimen (In.64045, Fig. 76) is placed in this extant family of weevils on the basis of the position of its head. This is tucked in under the pronotum with the rostrum lying along the ventral part of the body (Fig. 76). If the species had been prognathous with the rostrum



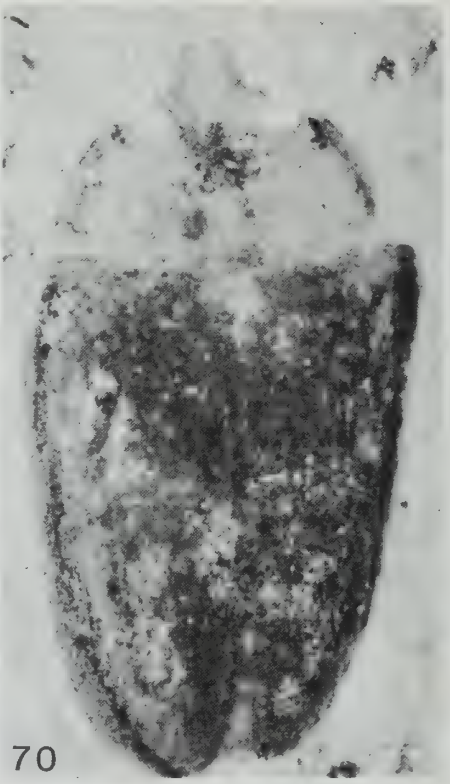


Fig. 69 Carabidae (?) species (Coleoptera). In.51040, 6·0 mm long.
Fig. 70 Carabidae (?) species (Coleoptera). In.49572, 5·5 mm long.

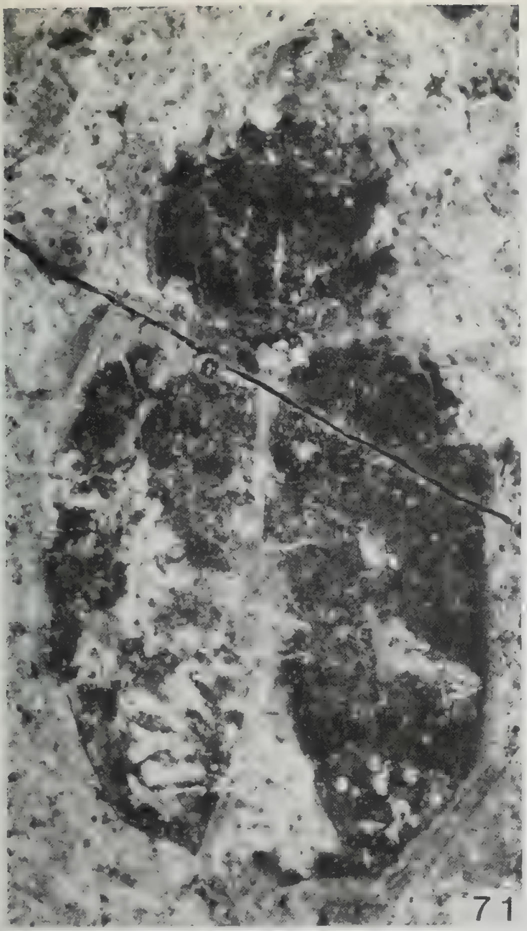
outstretched then it would have been unlikely to have been preserved with the head and rostrum under the body. On the strength of this it is provisionally placed in the Curculionidae. Although undoubtedly a weevil, few other features can be seen on the specimen which is therefore not classified further. Previously, weevils have been recorded from the Lower Cretaceous and Upper Jurassic (Arnoldi 1977); other Mesozoic weevils from the Upper Jurassic/Lower Cretaceous are described by Whalley & Jarzembowski (1985), but the Dorset specimen, from the Obtusum Zone, is the oldest known example.

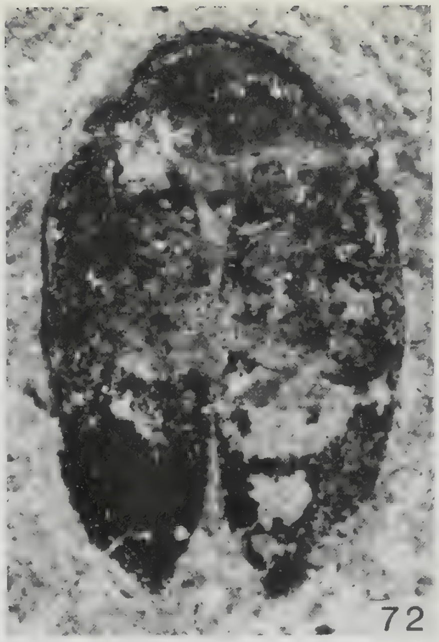
COLEOPTERA, *INCERTAE SEDIS*

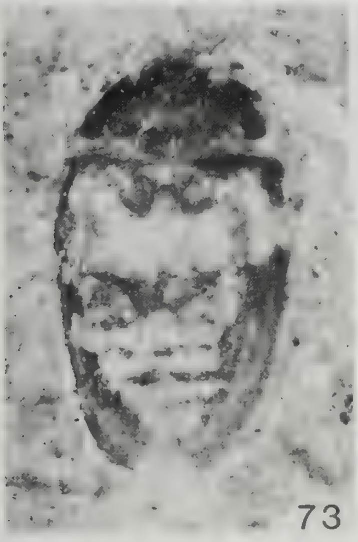
Family uncertain

There are a further 15 specimens which are fairly distinctive and can be differentiated from the other Coleoptera described but cannot be associated with any Recent family. There are a large number of fossil families, particularly from the Russian Jurassic, with which these have been compared but no satisfactory association can be made. They are separated into 12 species-groups which are considered in the general analysis of the fauna as representing distinct species.

Species 1, In.53967 (Fig. 78).
Species 2, In.59396 (Fig. 77).
Species 3, In.49238, In.49603, In.51020, In.51045.







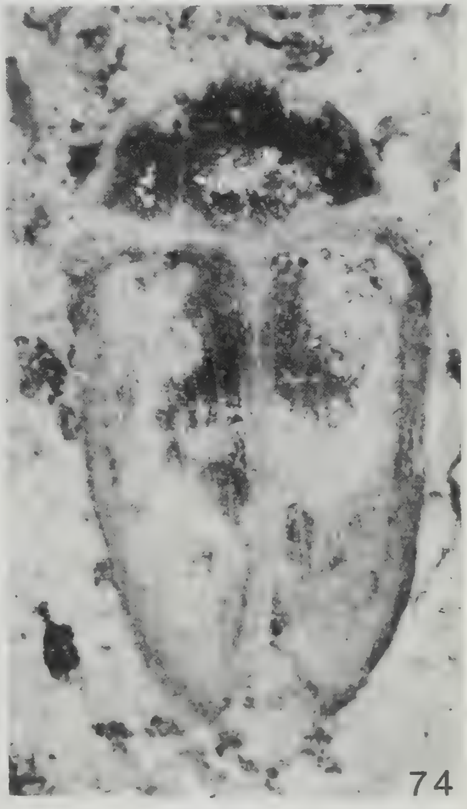
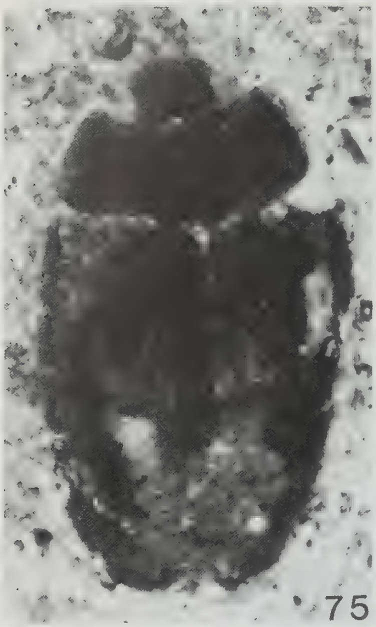


Fig. 71 Carabidae (?) species (Coleoptera). In.49222, 11·0 mm long.
Fig. 72 Byrrhoidea (?) species (Coleoptera). In.64021, 7 mm long.
Fig. 73 Dryopoidea (?) species (Coleoptera). In.59101, 5 mm long.
Fig. 74 Dryopoidea (?) species (Coleoptera). In.51009, 4·7 mm long.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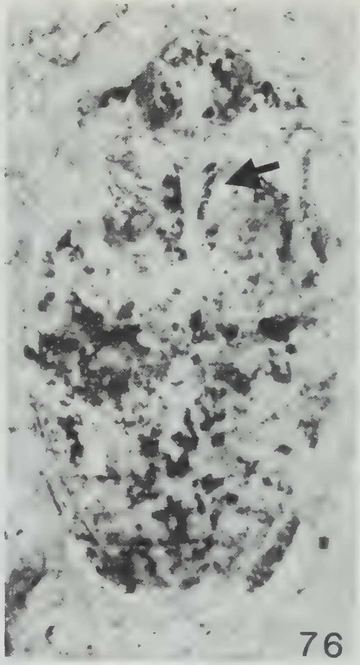
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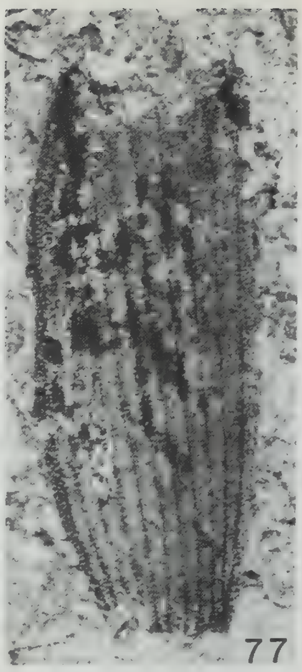
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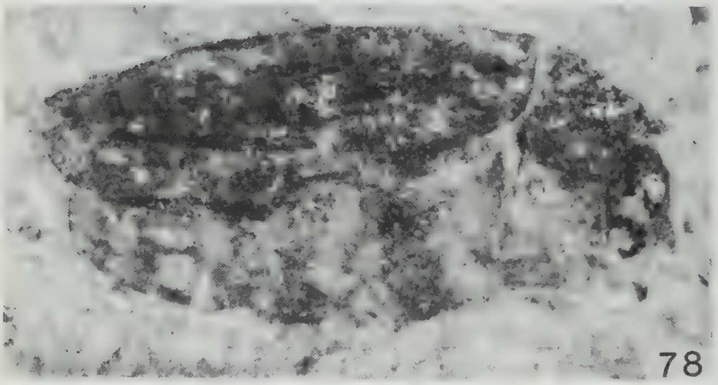
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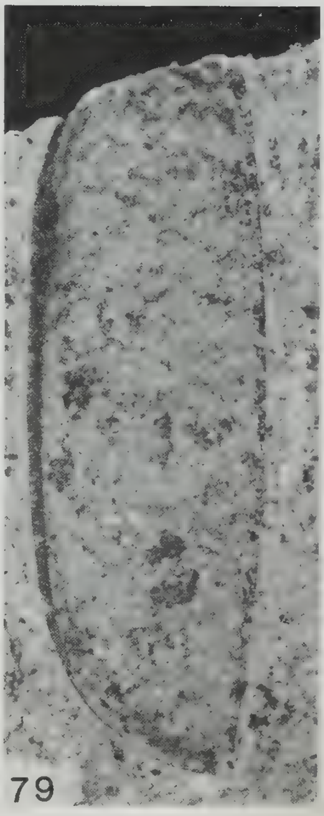
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Fig. 75 Dryopoidea (?) species (Coleoptera). In.64024, 5·5 mm long.

Fig. 76 Curculionidae gen. et sp. indet. (Coleoptera). In.64045, beetle length 5·5 mm. Arrow indicates the rostrum.

Fig. 77 Coleoptera species 2. In.59396, 10 mm long (incomplete).

Fig. 78 Coleoptera species 1. In.53967, 5 mm long. Fossilized in lateral position.

Fig. 79 Coleoptera species 10. In.59362, 14 mm long.

Species 4, In.49571.
Species 5, In.53961.
Species 6, In.49242.
Species 7, In.53977.
Species 8, In.59949.
Species 9, In.59150.
Species 10, In.59362 (Fig. 79).
Species 11, In.59389 (Fig. 80).
Species 12, In.59132, cf. *Omma liassica* Crowson, from the Upper Lias, Warwickshire (Fig. 81).

Family uncertain

The final group of beetles considered are curious, in that while we have many specimens we still do not know their relationship with Recent families.

Zeuner (1962) compared them in general appearance with species of *Tenebrio* (Suborder Polyphaga) or *Feronia* (Suborder Adephaga). Superficially the elytral patterns can be compared with Recent species of *Julodis* Eschscholtz (Suborder Polyphaga, Buprestidae), but *Julodis* species are much larger than the species discussed below. A further suggestion for a Recent family in which they might be included is the Melyridae, where some of the species have ridged elytra (B. Levey, personal communication). However, the pattern of lines on the elytra clearly joins up in the fossils whereas in Melyridae the ridges are separate. Insufficient specimens with the head and thorax have been found to make a reliable assessment of their systematic position but specifically they are very distinct. These beetles are known only from the English Lias and Rhaetic where they are not only conspicuous but relatively abundant.

Genus ***HOLCOPTERA*** Handlirsch, 1906

[= *Holcoelytrum* Handlirsch, 1906]

Type species. *Harpalus schlotheimi* Giebel 1856, by monotypy (Handlirsch 1906: 453). Upper Triassic–Lower Jurassic, U.K.

Handlirsch (1906) erected both *Holcoptera* and *Holcoelytrum*, but Cockerell (1915: 480) synonymized the two names, clearly giving the priority to *Holcoptera*. Zeuner (1962: 167), however, overlooked this, preferring *Holcoelytrum*, which was reasonable on account of the loss of the type specimen of *Holcoptera schlotheimi*. Cockerell's designation and synonymy, however, have priority, and furthermore we now have the neotype for the type species of *Holcoptera* designated by Zeuner (1962).

These are very distinctive and strongly patterned beetles, and although fragmentary specimens of the genus are not easily separated into species, the generic identity of even a small piece of a *Holcoptera* is easily recognized. It is possible such fragments could be used as stratigraphic indicators.

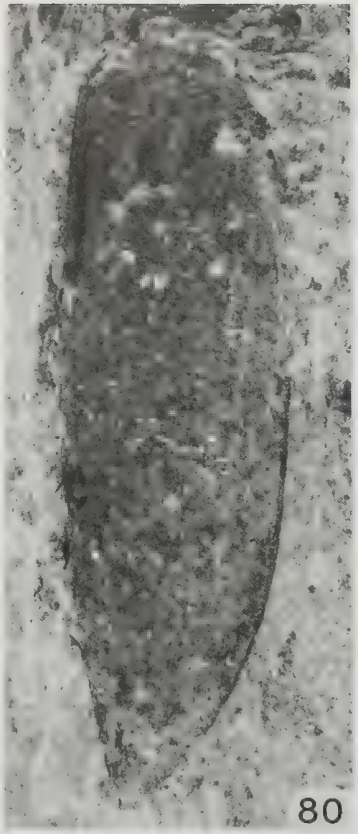
Holcoptera schlotheimi (Giebel 1856)

Fig. 82

1845 (Harpalideous Carabidae) Brodie: 101, 124; pl. 6, fig. 28.
1856 *Harpalus schlotheimi* Giebel: 63.
1906 *Holcoptera schlotheimi* (Giebel) Handlirsch: 453; pl. 41, fig. 63.
1915 *Holcoptera schlotheimi* (Giebel); Cockerell: 480.
1962 *Holcoelytrum schlotheimi* (Giebel); Zeuner: 170; pl. 27, fig. 5.

Diagnosis. Elytron over 5 mm long, with four black stripes (Zeuner 1962: 170).

Description. Eyes prominent, head protruding between eyes, rounded in front. Prothorax broader than long, possibly with median suture. Elytra with broad black stripes, possibly remnants of thicker part of elytra. Black stripes usually thinner than white, often with broader, angled part towards anterior end of elytra.



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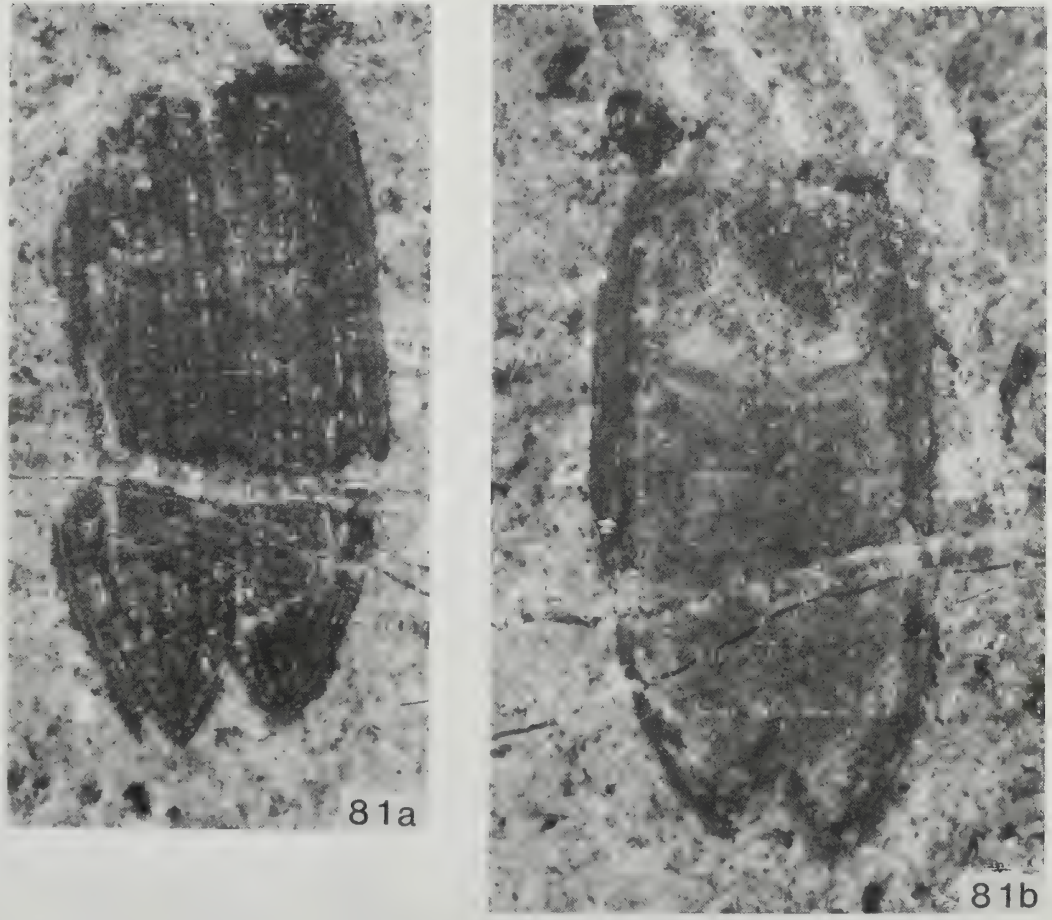

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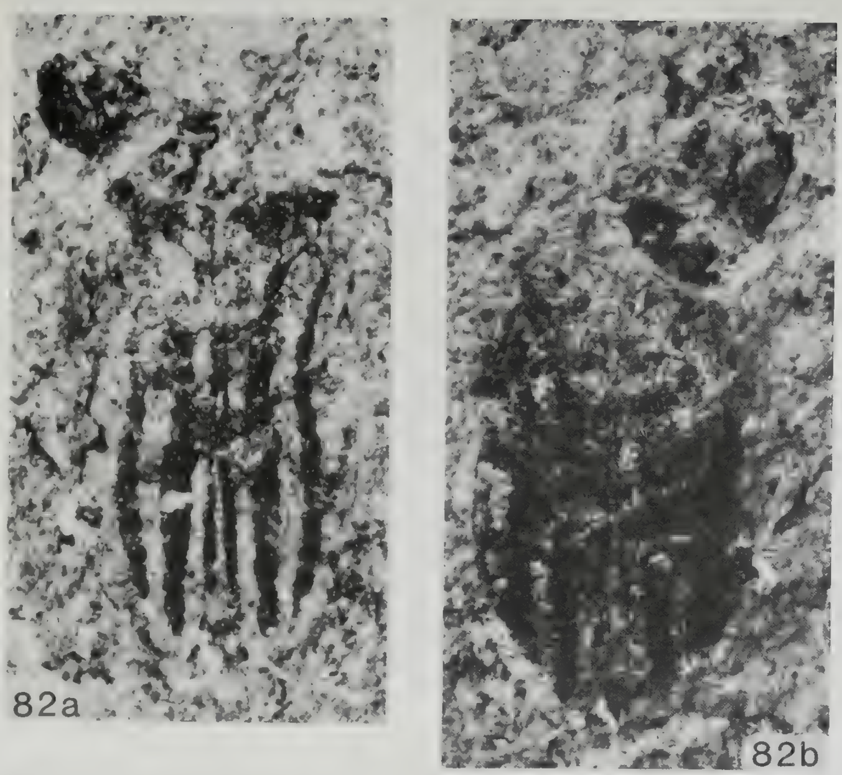
Fig. 80 Coleoptera species 11. In.59389, 20 mm long.

Fig. 81 Coleoptera species 12, cf. *Omma liassica* Crowson. In.59132, 7·7 mm long. Note contrasting preservation of part and counterpart; fossil split between elytra and rest of body. a, part. b, counterpart.



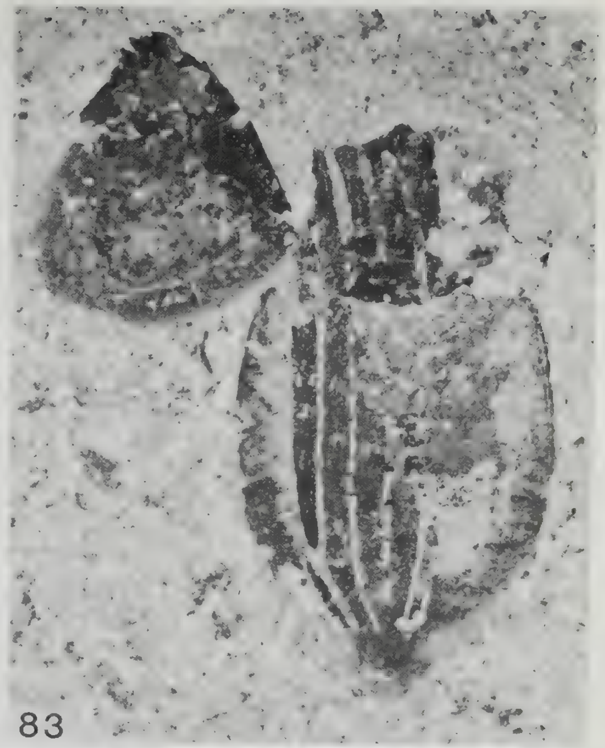


Fig. 82 *Holcoptera schlotheimi* (Giebel) (Coleoptera). In.53990, elytra 5–6 mm, total length of insect 7–8 mm. a, part. b, counterpart. Specimen listed by Zeuner, 1962: 170.

Fig. 83 *Holcoptera giebeli* (Handlirsch) (Coleoptera). In.53937, part, elytra 12 mm long. See Fig. 84.

NEOTYPE. In.59115; Flatstones, Charmouth, Dorset. Jackson colln. Designated by Zeuner, 1962.

ADDITIONAL MATERIAL. Additional to that listed by Zeuner, 1962: In.51019, In.53958, In.59115, all from Dorset. One further specimen, *ex* Brodie colln, locality uncertain, U.K. (probably Aust, near Bristol), in U.S. National Museum, cat. no. 61406. Seven specimens, Aust, near Bristol (Rhaetic), in Yorkshire Museum.

DIMENSIONS. Total length, 7·5–8 mm; elytra 5–6 mm.

DISCUSSION. This species is smaller than *H. giebeli.* It is also much less common, only five specimens being known from Dorset whereas there are 47 specimens of *H. giebeli. H. schlotheimi* appears in the Rhaetic in the U.K. and there are more specimens from the Lower Lias of Gloucestershire and Worcestershire. There are a number of Brodie specimens in other museums both in Britain and abroad, and it is possible that Giebel's type specimen may yet be found. It is unfortunate that Zeuner selected as neotype a specimen from Dorset when there are more specimens available from nearer the original type locality and from the same zone as the holotype.

From the similar sized *H. confluens* Cockerell, *H. schlotheimi* can be distinguished by the narrower and more parallel-sided black stripes. Its exact relationship with *H. confluens*, which is known by a few specimens from the English Lias, is not clear.

Holcoptera giebeli (Handlirsch 1906)

Figs 83–87

1845 (Harpalideous Carabidae) Brodie: 101, 124; pl. 10, fig. 2.
1856 *Harpalus schlotheimi* Giebel: 63 (*partim*).
1906 *Holcoelytrum giebeli* Handlirsch: 453; pl. 41, fig. 64.
1915 *Holcoptera giebeli* (Handlirsch) Cockerell: 480.
1962 *Holcoelytrum giebeli* Handlirsch; Zeuner: 168; pl. 27, figs 6–8.

DIAGNOSIS. Elytron over 10 mm long, with five black stripes (Zeuner 1962: 168).

DESCRIPTION. Thorax broad, slightly pointed on posterior margin. Prothorax probably divided. Strongly patterned black and white stripes on elytra, forming complete margin round elytra with central stripes joined posteriorly. Abdomen broad.

HOLOTYPE. I.3581 (Gloucestershire); Brodie colln.

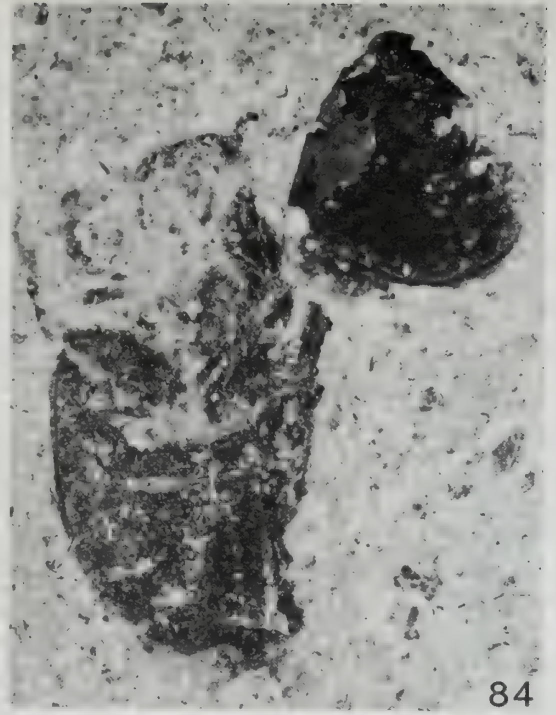
OTHER MATERIAL. Zeuner (1962: 168) listed 43 specimens from the Dorset Lias. There are four additional specimens from the Jackson collection, not listed by Zeuner: In.49618, In.51019, In.53921, In.53927. Also I.10977, Strensham, Worcestershire; Brodie colln (Upper Trias).

DIMENSIONS. 11·8–14 mm, elytra only.

DISCUSSION. Although there are more specimens of this species in the Dorset Lias than of *H. schlotheimi*, they are all incomplete, lacking the head and in most cases the thorax.

Discussion

Zeuner (1962) drew attention to the similarity he considered was shown by the conditions in Dorset in the Lower Lias and mangrove swamps of present-day tropics. This analogy was based on the absence of wave action and the sedimentation under protected conditions, with the presence of a marine element indicating tidal flow. He also considered that the mixture of marine animals and insects might have indicated that the Jurassic sea was of low salinity in the area. He discussed this concept in some detail with an analysis of various present-day brackish water insect faunas. He considered the deposits could represent a brackish water environment with access to the sea. He suggested that there was evidence for extreme waterlogging of the insects, caused by prolonged drifting and slow sinking: this was demonstrated by the state of the specimens in the deposit, with, for example, the beetles being compressed dorsoventrally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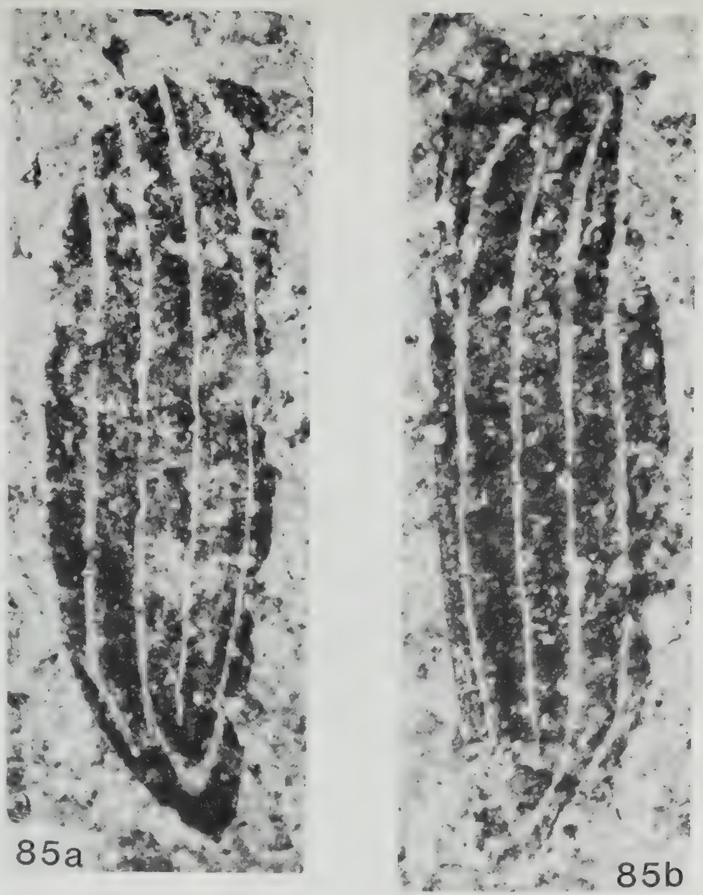
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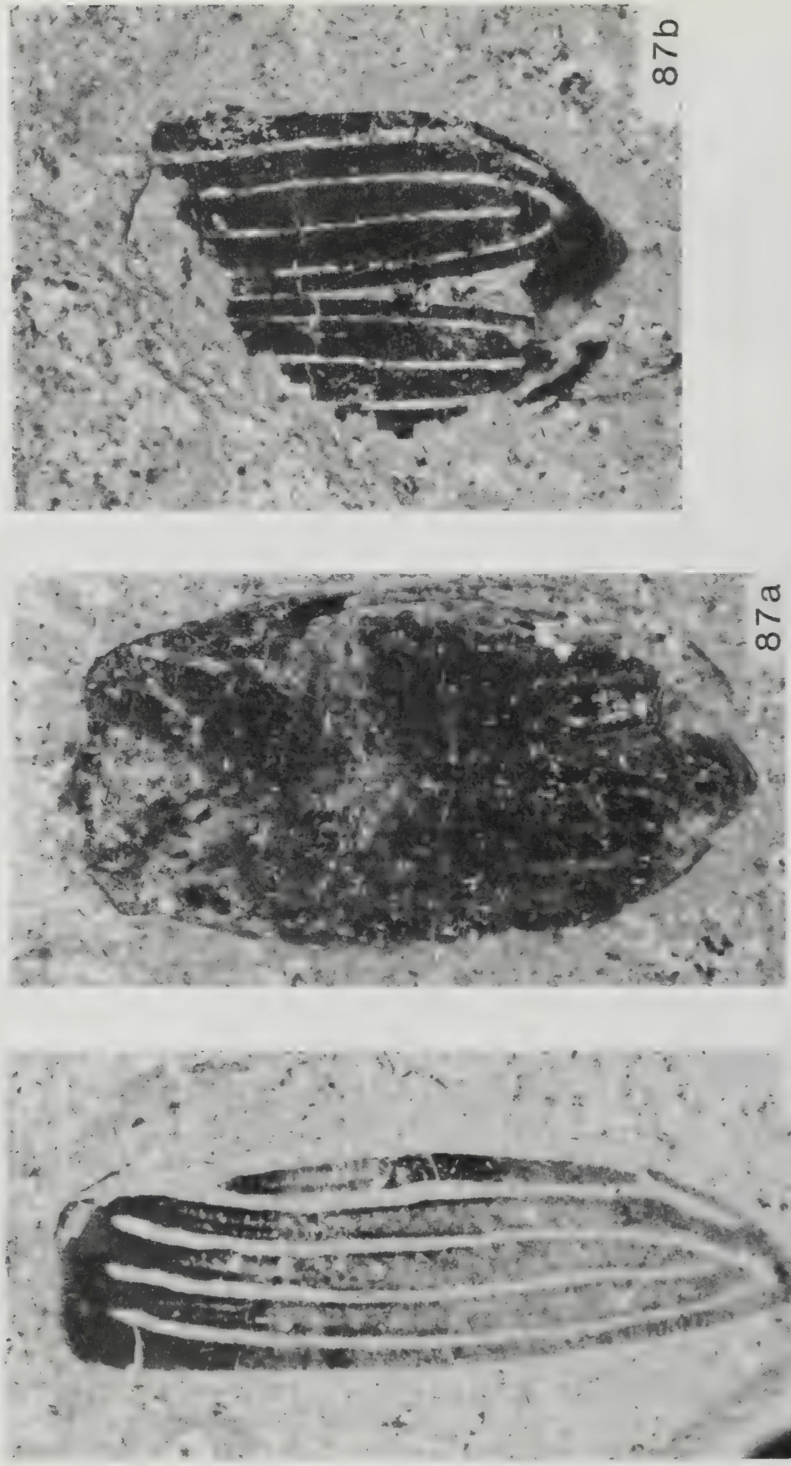
Figs. 84–85 *Holcoptera giebeli* (Handlirsch) (Coleoptera). Fig. 84, In.53937, counterpart, elytra 12 mm long. See Fig. 83. Fig. 85, In.53989, 11 mm long. a, part. b, counterpart.



Figs 86–87 *Holcoptera giebeli* (Handlirsch) (Coleoptera). Fig. 86, In.53981, 13 mm long. Fig. 87, In.53928, 12 mm long. a, part. b, counterpart.

and with wrinkles, indicating that they were wet and decaying when gradually compressed by the sediment. While a few beetles have been found with folds and wrinkles, many are in fact preserved with no dorsoventral flattening or evidence of decay. Some specimens clearly show firm compaction by the calcareous mudstone, but relatively few are distorted by movement of mud, either during or after burial. On the other hand, the twisting or folding of delicate wings is most likely to have occurred when they were very wet and, while the particular examples cited by Zeuner as evidence of waterlogging are not good, there is no doubt not only that the majority of the insects were waterlogged but that some were subject to mechanical disintegration. Curiously at least 40% of the beetles are represented by paired elytra, usually in close proximity or touching. This clearly shows that they must have remained associated until they arrived at the point where they were fossilized. Some of the specimens are not even disarticulated and have limbs attached. All this points to very tranquil deposition in the final stages.

As further evidence of transport and long periods of waterlogging, Zeuner (1962: 159) cited the condition of the dragonfly *Petrophlebia anglicanopsis*, which he said had 'its margins characteristically frayed as in modern insects that have begun to decompose in water'. He figured this specimen (1962: pl. 24, fig. 1) where it can be seen that it is pressed up against an ammonite shell. Removal of the shell (Fig. 8a, p. 123) has shown it is a complete, if slightly crumpled, wing. Very few of the specimens from Dorset in fact look as though they have suffered from prolonged waterlogging and *fraying*; most have remarkably complete margins.

There is nothing in the present study that supports Zeuner's 'mangrove' hypothesis, although there is only negative evidence against it. Few, if any, of the species found would be regarded as characteristic of the specialized 'mangrove' habitat, but there is nothing against the idea that the insects were brought down in the rivers that fed the swamps and then deposited in the more tranquil 'mangrove' conditions. One would, however, have expected more of the 'mangrove' fauna (which in the Lower Jurassic would not have been an angiosperm-type mangrove community) to have been fossilized *in situ* as well. There is no evidence to suggest that the insects were deposited on a tide-line; in fact the extremely fine sediment, gently laminated, would indicate an area of undisturbed mud, certainly not a tide-line. Furthermore the insects are not deposited in concentrations, although a few were fossilized together; mostly they are well separated in separate blocks.

Zeuner stated (1962: 155) that the 'preliminary classification of the specimens . . . has shown that both in composition of the fauna and in the preservation they resemble those of the Lower Lias of Gloucestershire, Warwickshire, and Worcestershire, though there are some significant differences'. The main problem in comparing these two faunas is that the Lower Lias of Gloucestershire and Worcestershire has not been studied critically, except for the Orthoptera, since they were first described. The present study contradicts Zeuner's views strongly and shows that the two faunas were dissimilar, with few species in common, but a critical analysis will have to await a study of the West Country and Midlands Liassic fauna. The insects of the two areas are not the same age: those from the Obtusum Zone of Dorset are stratigraphically younger than those of the West Country, which are mostly Rhaetic or lowermost Liassic (Planorbis Zone). Whalley (1982: 147) briefly compared the two areas, and concluded that their ecological origins were different. Zeuner (1962: 159) discussed the question of the origin of the Dorset fauna. He ruled out the idea that the mud in which the insects had been originally buried had dried out and then been reworked, with the specimens washed out and redeposited, on the grounds that the deposit would then have been in belts of concentrated fragments of vegetation, marine animals and insects. He concluded that this was an area of calcareous mud near land, where insect flotsam was deposited at random in a wave-free, protected environment. He also ruled out that wind could have transported living insects, which then got stuck in the exposed mud. There are very few complete insects which could have landed on mud and been fossilized *in situ*.

Probably the most complete insects are the rather tough waterbugs, some of the Orthoptera and one or two of the rather delicate orthophlebiids. More of the beetles have a few articulated parts but there are a great many isolated elytra. Many of the specimens are represented by a single wing; in a few cases these too are torn or heavily folded. All this indicates mechanical damage to the insects after death. In contrast, in the case of the scale-covered wing of *Archaeolepis* very little mechanical action would be needed to remove the scales which are inserted in sockets in the wing. There are, too, the relatively complete 'sets' of wings, for example the dragonfly (in private hands) or the orthophlebiid (Fig. 47), which cannot have been transported far. There is some evidence that dead insects will float on still water for several weeks (E. A. Jarzembowski, personal communication) and might well be carried some distance before breaking up. The separate parts could then be carried further; for example, individual wings are particularly tough until waterlogged or weakened by fungal or bacterial action, and it is only then that the wing will tear readily—while still unwaterlogged they can resist considerable mechanical damage. There is a difference in the rate of waterlogging, depending on whether the insect was dead and partly dried when it fell in the water or whether it landed in it alive; in the latter case waterlogging and fungal attack are more rapid. Fungal attack usually takes place in fresh water; there is less evidence of its action in salt water. The distance a wing or a whole insect may travel on or in water depends on many factors. Insects with abundant hairs or scales will trap air and may resist wetting for longer after immersion. Assuming an insect avoids being eaten as it is washed along, and this is probably the fate of many that fall into water, it is likely to be damaged more rapidly if it is carried on the water surface where this is broken by wind, waves or the presence of rocks. At certain current speeds, as yet not exactly determined, dead insects *in* a current will not hit large stationary objects (e.g. rocks) as they are swept along below the surface. Thus an entire insect may be gently eased round obstructions by the current flow, where larger objects may be damaged by striking them. Surface tension is also important in the early stages. This may be affected not only by factors already mentioned but also by the nature of the dissolved chemicals in the water, as a degree of natural saponification of debris will materially lower the surface tension and facilitate the wetting of dead insects. Probably the pH of the water, which obviously reflects the chemical content, also affects an insect transported by the current.

Zeuner (1962) was correct in suggesting the Dorset insects were deposited under tranquil conditions. The fine-grained rock is relatively evenly bedded, with little sign of surface disturbance or scourfills, and there is no evidence of concentration of insect fossils other than by obstruction, i.e. where they have been washed up against pieces of wood or an ammonite shell.

Allowing for possible differences in the geographical or ecological origins of the insects in the Dorset fossil assemblage, certain hypotheses can thus be proposed about their origins and the environment from which they were derived. These are listed under three main headings below.

1. **Fresh water**. The aquatic Heteroptera were from non-saline water; this fresh water would also have been needed by the immature stages of all the dragonflies. Although a number of modern dragonflies are migratory and are often found far out at sea, the majority are territorial and do not have a migratory adult phase. Some of the Coleoptera fossils are water beetles and although the adults were probably able to fly they would still have needed fresh water for the immature stages and for much of their adult life. Thus a source of fresh water was needed for some of the insects which, judged from the condition of the specimens, was not far away from the site of fossilization. The fresh water could have been a lake or a river (or both), although it is interesting that no Ephemeroptera or Trichoptera, both of which have aquatic larvae, were found in the fossil assemblage.

One of the belostomatid water bugs (new species 8A, Fig. 42 and p. 146) is in such good condition that it could have flown in; if it was washed in, it is unlikely to have been carried far since there is the minimum of mechanical damage to the insect. There is no sign of fungal damage, which can begin within a week of death in fresh water (E. A. Jarzembowski, personal communication). There was, therefore, a fresh water source for the Dorset Lias—and hence some land—within a few miles, especially since the belostomatids are not noted for long-distance flights.

2. **Marine**. Few insects are truely marine, although a number will tolerate brackish water. Most of the insects in the Dorset fossil assemblage are unlikely to have been dependent on a marine

environment: possibly some of them scavenged on the shore-line but the majority are wholly terrestrial in origin. The environment in which the insects were fossilized is always regarded as completely marine, as evinced by the presence of ammonites. But perhaps ammonites could have been carried into estuaries by tide and wind and have been deposited in a far less saline environment: the modern nautiloid shell will float and certainly gets washed up onto beaches. There is, however, no evidence of a shore line associated with the insect and ammonite fossils and the total absence of fossilized aquatic insect larvae, which are known from other deposits, make it very unlikely that the deposition zone was other than fully marine.

3. **Terrestrial**. There is nothing in the constitution of this particular thanatocoenosis, other than the straight terrestrial/aquatic habitats, to indicate that the insects were *all* derived from the same environment. Certain general facts can be inferred from the species content of the assemblage. The presence of a large and diverse Orthoptera population, with bush-crickets and true crickets predominating, does at least indicate that these were derived from an area where the vegetation was varied; it was more likely to have been an open bush area with trees than the dense shore-line vegetation suggested by Zeuner (1962). The bush-crickets no doubt lived amongst the leafy vegetation of the Filicales which were abundant in the Upper Jurassic (Harris 1961), and these together with the Bennettitales, Cycadales and Coniferales, which have all been recorded from the Lias of Dorset, provided the plants on which the insects lived and fed (Seward 1904). No angiosperms have been reported (Hughes 1976). The presence of numerous dragonflies, apart from indicating non-saline water sources, also suggests that the area from which they were derived was fairly open, rather than densely wooded. Such an abundance of aerial predators also points to an abundant source of food for them. There is no evidence to suggest that the dragonflies were other than predators of flying insects, like Recent species, and there must have been a good source of flying insects which they caught. No doubt many of these were the orthophlebiids which are common in the fossil record, and which, from their appearance and by analogy with present-day Mecoptera, were probably not strong fliers.

Comparison with other Mesozoic faunas

1. **British Mesozoic**. There are extensive insect faunas in the British Lower and Upper Jurassic (e.g. Warwickshire, Worcestershire, Dorset) but none has been recently monographed. Preliminary studies (Whalley 1982, 1983) show that, apart from the relative ages, there are fundamental differences between the Dorset Lower Lias and the others, sufficient to indicate that they were drawn from ecologically different sources.

An initial comparison of the Lower Cretaceous (Wealden) fauna with the Dorset Lias shows that the proportion of extinct families is much higher in the Liassic fauna (E. A. Jarzembowski, personal communication).

2. **Continental Europe and Asian Mesozoic**. The data from two continental European and one Asian fauna were examined and tabulated (Table 2). The Upper Liassic fauna from eastern Lower Saxony was studied by Bode (1953). He described over 300 new species from the collection, recognizing only 15 previously-described species six of which he had described earlier from the same locality in Saxony. The insect fauna was rich in Homoptera but Coleoptera were again the most numerous, although the percentage of beetles in the total fauna was lower than in the Dorset Lias (27·4% Saxony; 39·0% Dorset). The percentage of species of Heteroptera was higher in the Dorset Lias than in the other three faunal assemblages (Table 2) but they had more Neuroptera and Diptera.

Since the Dorset figures in Table 2, apart from other variables, do not represent an exactly contemporary fauna, too much must not be read into the figures. Differences in the assemblages are likely to be caused by a number of factors, the two primary ones being the differences in age (Lower Lias, Upper Lias, Upper Jurassic) and ecological difference in the areas from which the insect fossils were derived. To emphasize the caution needed in considering these figures, the similar percentages for Orthoptera should be examined in more detail. The Dorset Lower Lias has 14% while the Upper Lias (Saxony) site has 15%, but the species composition is quite

Table 2 Percentage of species in each family. Saxony and Dobbertin data from Bode (1953); Karatau data from Rohdendorf (1968).

	Dorset Lower Lias	Saxony Upper Lias	Dobbertin Upper Lias	Karatau Upper Jurassic
Ephemeroptera	—	—	—	0·3
Blattodea	3·1	1·3	0·2	3·4
Orthoptera	14·0	15·0	20·7	2·4
Dermaptera	1·5	—	—	0·6
Odonata	10·9	6·5	6·2	10·0
Plecoptera (*s. l.*)	—	2·2	0·7	—
Heteroptera	14·0	7·3	6·2	4·8
Homoptera	6·2	18·6	21·5	4·5
Psocoptera	—	—	—	0·6
Thysanoptera	—	—	—	0·3
Raphidioptera	3·1	—	—	2·4
Neuroptera	—	6·5	4·6	4·1
Mecoptera	4·6	5·9	9·3	2·4
Trichoptera	—	0·5	8·8	1·0
Lepidoptera	1·5	—	—	—
Diptera	1·5	7·9	11·9	22·5
Coleoptera	39·0	27·4	9·3	21·1
Hymenoptera	—	—	—	18·7

different. In the Dorset Lias the family Gryllidae predominated while in the Saxony fauna it was the Elcanidae.

One of the differences between the faunas is the total absence of Trichoptera, Plecoptera (*sens. lat.*) and insect larvae from the Dorset Lias. This certainly indicates a different ecological source for the faunas. Probably the most striking difference is between the Lower Jurassic (the Liassic faunas) and the Upper Jurassic. The proportion of Diptera has virtually doubled in the Upper Jurassic, while a large number of Hymenoptera have appeared. It is possible to argue that, apart from the age, the appearance of Hymenoptera in the fauna is due to the specialized area from which the assemblage was derived; Hymenoptera have not, however, been found in many Lower Jurassic sites. The high proportion of Diptera and Hymenoptera, and even of Neuroptera, may indicate a derivation of the Upper Lias assemblages from areas more wooded than that of Dorset.

Lin (1976) studied a small Middle/Upper Jurassic fauna from China where the composition of the fauna was broadly similar to the European sites (for example in the absence of the Trichoptera), but there were more Diptera and a smaller proportion of Orthoptera.

Palaeogeography

Although there were four land masses in the Sinemurian which bordered the 'Western Approaches – English Channel' (Ziegler 1982, Naylor & Shannon 1982), only the Cornubian (or Cornish) Massif is considered to be a likely land-source for the insects which fossilized in Dorset. The other land masses, the London–Brabant Massif, Armorican Massif and Welsh High, are considered to have been too far away. In the palaeogeographic maps produced, the Western Approaches Island (Hallam 1975), and the Cornish Platform (Naylor & Shannon 1982) or Cornubian Massif (Ziegler 1982), are not extended as far south-eastwards as suggested by the evidence from the insect fossils.

The ecological (and age) difference which is apparent between the Dorset and Midlands Lias indicates either that these two faunas were derived from different areas, or if they were derived from the same land mass, that the age difference (about 5 million years) had brought about ecological changes. The age difference between the Midlands Lias and Dorset Lias is between the Upper Sinemurian (Obtusum Zone, Dorset) and the Hettangian (Planorbis Zone, Midlands). From the palaeogeographic map of Ziegler (1982) it is possible to consider that the proximity of the Welsh Massif to the Midlands could have provided their fossil assemblage and that the Cornubian (Cornish) Massif provided the Dorset assemblage. As an indication of the different ecological origins of the faunas from the two zones, one of the clearest examples is the orthopterous family Bintoniellidae. This family is abundantly represented in the Lower Lias of the Midlands and occurred in the Lower Sinemurian (Bucklandi Zone), 67 km south of Plymouth (Whalley 1982). The family is absent from Dorset where the Orthoptera are well represented by other families.

The relatively undamaged landbugs (Family nov. 1, p. 143) and almost complete waterbug (new species 8A, p. 146) must have flown in, or only been carried a short distance by currents. The wing of the moth-like *Archaeolepis* (Fig. 58), preserved with scales attached, again indicates the presence of a land source within 50 miles and probably much nearer. Naylor & Shannon (1982: 138) pointed out that occasional deltaic complexes built up in the seas, and, although they were less well developed adjacent to the Cornubian Massif, these must also be considered as possible sources of the fossilized insects.

Two hypotheses are proposed from this study; either the land mass was within 80 km of the present site of Charmouth in the Lower Sinemurian, or the land was near to this site only once, for a period of some 300,000 years in the Sinemurian. In the whole of the succession at Charmouth, the calcareous mudstone and shale in which the fossils have been found is relatively uniform, with evidence of deposition over a long period under fairly tranquil conditions. However, all the insects and the larger pieces of plants are found in only two adjacent strata, the Obtusum Zone and the Turneri Zone (where some of the insects occur in the Birchi nodules). Thus for some reason there was only one period of some 300,000 years when the land was near enough for the insects to be deposited; the only alternative to this is that the deposition currents changed completely. There is no obvious evidence for major changes in condition of deposition of the marine animals, which might suggest a current change in the area. Therefore, either there were massive changes on the land preventing deposition of more insects, or the land itself receded. Even though the insects are only fossilized in the calcareous nodules and have not been found evenly distributed along the various zones, they are still restricted to these particular zones, in spite of there being many more metres of fine, apparently undisturbed sediment.

I favour the hypothesis of a closer proximity of the Cornubian Massif in the Lower Lias and of its proximity being for a relatively brief period. The conditions under which the sediments and remains of the fauna were accumulating in the Charmouth area need to be reconsidered. The sediments were probably laid down in shallow water, not far from land. The presence of marine ammonites and well-preserved insects in the same deposit indicates that tranquil conditions existed at those horizons in which the insects are now found. It is possible that a land area within a few miles and periodic (? tidal) emergence of the seabed would explain the close juxtaposition of the ammonites and insects.

Phylogeny

Most of the phylogenetic implications are discussed in the systematic section and only a few will be enlarged upon here.

With few exceptions the Dorset Liassic insect fauna was more akin to earlier faunas than those of the Lower Cretaceous and represented the first insect stage of the Mesozoic. Insect fossils from the Cretaceous are dissimilar and can often be placed in Recent families (E. A. Jarzembowski, personal communication), whereas the majority of the species from Dorset belong to extinct families. This points to a major change in the insect fauna between the Lower Jurassic and the Lower Cretaceous, at which some modern families appeared. A similar change in the marine faunas at the Toarcian transgression produced a dramatic change in the faunas (Ager 1983), but the species composition of the land flora in the gymnosperms and ferns did not change, although the proportion of the species in the flora probably did (C. R. Hill, personal communication). Changes seem to have really commenced with the very first appearance of the angiosperms. In a few groups of insects with modern representatives that are also found in the Jurassic, like the anisozygopteran dragonflies or the tettigarctid cicadas, there are many Mesozoic species but very few Recent ones: in fact only two living species in both these groups. In others, such as the freshwater Heteroptera, some of the elaterid beetles and the crickets there are few species in the Lower Jurassic but they can be placed in extant families that are now very diversified. We thus have two extremes in the Lower Lias: on the one hand families showing great diversity but which became extinct or very reduced in diversity by the Cretaceous, and on the other families represented by few examples in the Lower Lias but whose increase in diversity began in the Cretaceous and has continued with time. With the belostomatid waterbugs it is easy to appreciate that the ancestors of this group were able to migrate from the Old World to the New World in the Mesozoic before the continents were widely separated. It is interesting that while the waterbugs are the earliest representatives of Recent families, all the landbugs described from Dorset represent extinct families, and exactly the same phenomenon was found by Popov & Wootton (1977) in the Upper Lias of Saxony.

Unless a species was well adapted to its own environment it would not have 'survived' to be fossilized. Many of the Liassic fossils show a high degree of specialization, comparable in many cases with Recent faunas. For example the Jurassic cricket *Regiata scutra* sp. nov. (Fig. 19 and p. 131) had a typical rolled wing tip (at rest) and the highly specialized venation associated with sound production found in Recent crickets. These highly specialized forms died out and were replaced by equally specialized new forms. A considerable environmental and ecological change must have occurred to render the insect fauna of the Lower Jurassic unsuitable for conditions in the Late Jurassic and Cretaceous.

The Dorset Lias gives us a glimpse of a highly specialized and successful insect fauna heading towards this transition from the older and now extinct families, but which includes a few early representatives of Recent families. The subsequent success of the latter can be judged from the abundance and diversity of the Recent insect fauna.

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The photographs were taken by the Photographic Unit, B.M.(N.H.); I appreciate the trouble they have taken with often very difficult material.

References

Ager, D. V. 1983. Allopatric speciation – an example from the Mesozoic Brachiopoda. *Palaeontology*, London, **26** (3): 555–565.

Arnoldi, L. V. 1977. *In* Arnoldi, L. V., Zherikhin, V. V., Nikritin, L. M. & Ponomarenko, A. G., Mezozoĭskie Zhestkokrȳlȳe [Mesozoic Coleoptera]. *Trudȳ paleont. Inst.*, Moscow & Leningrad, **161:** 1–204, 14 pls.

Asahina, S. 1954. *A morphological study of a relic dragonfly*, Epiophlebia superstes *Selys* (*Odonata, Anisozygoptera*). iv + 153 pp., 71 pls, 130 figs. Tokyo (Jap. Soc. Prom. Sci.).

Bekker-Migdisova, E. E. 1949. Mezozoĭskie Homoptera sredneĭ Azii [Mesozoic Homoptera of central Asia]. *Trudȳ paleont. Inst.*, Moscow, **22:** 3–67, 1 pl.

Bode, A. 1953. Die Insektenfauna des ostniedersächsischen Oberen Lias. *Palaeontographica*, Stuttgart, (A) **103** (1–4): 1–375, pls 1–15.

Brodie, P. B. 1845. *A history of the fossil insects in the Secondary rocks of England.* 130 pp., 11 pls. London.

Carle, F. L. 1982. The wing vein homologies and phylogeny of the Odonata; a continuing debate. *Rapid Commun. Soc. int. Odonatol.*, Utrecht, **4:** 1–66.

Carpenter, F. M. 1936. Revision of the Nearctic Raphidiodea (Recent and Fossil). *Proc. Am. Acad. Arts Sci.*, Boston, **71** (2): 89–157, pls 1–2.

—— 1967. Cretaceous insects from Labrador, 2. A new family of snake-flies (Neuroptera: Alloraphidiidae). *Psyche, Camb.* **74:** 270–275.

Cockerell, T. D. A. 1915. British Fossil Insects. *Proc. U.S. natn Mus.*, Washington, **49:** 469–499.

Coope, G. R. 1979. Late Cenozoic fossil Coleoptera: Evolution, Biogeography and Ecology. *A. Rev. Ecol. Syst.*, Palo Alto, **10:** 247–267.

Cope, J. C. W. ***et al.*** 1981. A correlation of Jurassic rocks in the British Isles. Part I. *Spec. Rep. geol. Soc. Lond.* **14.** 73 pp.

Cowley, J. 1942. Description of some genera of fossil Odonata. *Proc. R. ent. Soc. Lond.* (B) **11:** 63–78.

Davis, G. M. 1956. *The Dorset Coast, a Geological Guide.* 128 pp. London.

Dolin, V. G. 1975. [A contribution to the systematics of Mesozoic click beetles (Coleoptera, Elateridae)]. *Paleont. Zh.*, Moscow, **1975** (4): 51–62, pls 7, 8 (In Russian; Engl. transl. *Paleont. J.*, Washington, **9:** 474–486).

Dolling, W. R., Popov, Y. & Whalley, P. (In press). British Lower Jurassic Heteroptera.

Enderlein, G. 1906. The scaly winged Copeognatha. *Spolia zeylan.*, Colombo, **4:** 39–122, pls A–G.

Fraser, F. C. 1957. *A reclassification of the order Odonata.* 133 pp. Sydney, R. Zool. Soc. N.S.W.

Fujiyama, I. 1973. Mesozoic Insect Fauna of East Asia. Part 1, Introduction and Upper Triassic Fauna. *Bull. natn. Sci. Mus. Tokyo*, **16:** 331–386.

Gardiner, B. G. 1961. New Rhaetic and Liassic beetles. *Palaeontology*, London, **4** (1): 87–89.

Giebel, C. G. 1856. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere*, **2** (1). 511 pp. Leipzig.

Harris, T. 1961. *The Yorkshire Jurassic Flora*, **1.** Thallophyta–Pteridophyta. v + 212 pp. London, British Museum (Natural History).

Hallam, A. 1975. *Jurassic Environments.* 269 pp. Cambridge.

Handlirsch, A. 1906–08. *Die fossilen Insekten und die Phylogenie der rezenten Formen.* ix + 1430 pp., 13 tabs, 14 figs, 51 pls. Leipzig.

Haughton, S. H. 1924. The fauna and stratigraphy of the Stormberg series. *Ann. S. Afr. Mus.*, Cape Town, **12:** 323–497.

Heinrich, C. 1956. American moths of the Subfamily Phycitinae. *Bull. U.S. natn. Mus.*, Washington, **207.** 581 pp.

Hennig, W. 1981. *Insect phylogeny* (transl. Pont, A. with additional footnotes). xxii + 514 pp. Chichester.

Hughes, N. F. 1976. *Palaeobiology of Angiosperm Origins.* 242 pp. Cambridge.

Imms, A. D. 1970. *A general textbook of Entomology* (9th edn, Ed. Richards, O. W. & Davies, R. G.). x + 886 pp. London.

Jackson, J. F. L. 1926. The junction of the Middle and Upper Lias of the Dorset Coast. *Q. Jl geol. Soc. Lond.* **82:** 409–525.

Kovalev, V. G. 1982. [Some Jurassic Diptera–Rhagionids (Muscida, Rhagionidae)]. *Paleont. Zh.*, Moscow, **1982** (3): 88–100, pl. 9 (In Russian; Engl. transl. *Paleont. J.*, Washington, **16** (3): 87–99).

Kristensen, N. P. 1970. Morphological observations on the wing scales in some primitive Lepidoptera (Insecta). *J. Ultrastruct. Res.*, New York & London, **30:** 402–410.

—— 1975. The phylogeny of the Hexapod 'Orders'. A critical review of recent accounts. *Z. Zool. Syst. EvolForsch.*, Frankfurt a.M., **13:** 1–44.

—— 1979. A new family of Microlepidoptera from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera, Zeugloptera). *Steenstrupia*, Copenhagen, **5** (7): 69–147.

—— 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). *Steenstrupia*, Copenhagen, **10** (5): 141–191.

Lang, B. 1968. (Obituary of) James Frederick Jackson. *Proc. Dorset nat. Hist. archaeol. Soc.*, Dorchester, **89:** 18–19.

Lang, W. D. & Spath, L. F. 1926. The Black Marl of Black Ven and Stonebarrow in the Lias of the Dorset Coast. *Q. Jl geol. Soc. Lond.* **82:** 144–187.

——, —— **& Richardson, W. A.** 1923. Shale with 'Beef', a sequence in the Lower Lias of the Dorset Coast. *Q. Jl geol. Soc. Lond.* **79:** 47–99.

Lin Qibin 1976. [The Jurassic fossil insects from Western Liaoning]. *Acta palaeont. sin.*, Peking, **15:** 97–116, 3 pls (In Chinese, Engl. abstract).

MacLeod, E. G. 1970. The Neuroptera of Baltic Amber. Ascalaphidae, Nymphidae and Psychopsidae. *Psyche, Camb.* **77** (2): 147–180.

Martynov, A. 1925. To the knowledge of fossil insects from Jurassic beds in Turkestan. 1. Raphidioptera. *Izv. ross. Akad. Nauk*, Leningrad, (6) **19** (6–8): 233–246 (1925*a*). 2. Raphidioptera (continued), Orthoptera (s.l.), Odonata, Neuroptera. *Loc. cit.* **19** (12–15): 569–598 (1925*b*). (In English).

—— 1927. Jurassic fossil *Mecoptera* and *Paratrichoptera* from Turkestan and Ust-Balei (Siberia). *Izv. Akad. Nauk SSSR*, Leningrad, (6) **21** (7–8): 651–666 (In English, Russian summary).

—— 1928. A new Fossil Form of Phasmatodea from Galkino (Turkestan), and on Mesozoic Phasmids in general. *Ann. Mag. nat. Hist.*, London, (10) **1:** 319–328.

—— 1937. Liasovȳe nasekomȳe Shuraba i Kizil-Kii [Liassic insects from Shurab and Kisyl-Kiya]. *Trudȳ paleont. Inst.*, Moscow, **7** (1): 7–180, 5 pls.

Martynova, O. M. 1947. Dve novye verblyudki iz yursikh slantsev Karatau [Two new Raphidioptera from the Jurassic shales of Karatau]. *Dokl. Akad. Nauk SSSR*, Leningrad, **56** (6): 635–637.

—— 1961. Sovremennȳe i vȳmershie verblyudki (Insecta, Raphidioptera) [Recent and fossil snakeflies]. *Paleont. Zh.*, Moscow, **1961** (3): 73–83.

McAlpine, J. F. *et al.* (eds) 1981. *Manual of Nearctic Diptera*, **1**. 674 pp. Ottawa (Monograph 27, Research Branch, Agriculture Canada).

Naylor, D. & Shannon, P. 1982. *Geology of offshore Ireland and Western Britain.* 161 pp. London.

Ponomarenko, A. G. 1969. Istoricheskoe razvitie zhestkokrȳlȳkh–Arkhostemat [Historical development of Coleoptera–Archostemata]. *Trudȳ paleont. Inst.*, Moscow, **125**. 238 pp., 14 pls.

Popov, Y. A. 1971. Istoricheskoe razvitie poluzhestkokrȳlȳkh Infraotryada Nepomorpha (Heteroptera) [Historical development of Hemiptera of the Infraorder Nepomorpha (Heteroptera)]. *Trudȳ paleont. Inst.*, Moscow, **129:** 3–227, 9 pls.

—— **& Wootton, R. J.** 1977. The Upper Liassic Heteroptera of Mecklenburg and Saxony. *Syst. Ent.*, London, **2:** 333–351.

Pritykina, L. N. 1968. Strekozȳ Karatau (Odonata) [Dragonflies of Karatau]. *In* Rohdendorf 1968 (q.v.): 26–54, pls 2–5.

—— 1980. Otryad Libellulida. *In* Rohdendorf, B. B. (Ed.), Istoricheskoe razvitie Klassa Nasekomykh [Historical development of the Class Insecta]. *Trudȳ paleont. Inst.*, Moscow, **175:** 128–134, figs 67–69.

Ragge, D. R. 1955. *The wing-venation of the Orthoptera Saltatoria, with notes on the Dictyoptera wing-venation.* 159 pp. London, British Museum (Natural History).

Rasnitsyn, A. P. 1983. Pervaya nakhodka babochki yurskogo vozrasta [First find of a moth from the Jurassic]. *Dokl. Akad. Nauk SSSR*, Moscow, **269** (2): 467–471.

Riek, E. F. 1976. A new collection of insects from the Upper Trias of South Africa. *Ann. Natal Mus.*, Pietermaritzburg, **22:** 791–820.

Rohdendorf, B. B. 1962. [Arthropoda. Tracheata and Chelicerata.] *Osnovȳ Paleontologii*, Moscow, **9**. 560 pp. (In Russian).

—— 1964. (see 1974).

—— (Ed.) 1968. *Yurskie nasekomȳe Karatau* [*Jurassic insects of Karatau*]. 252 pp., 25 pls. Moscow, Nauka.

—— 1974. *The historical development of Diptera.* 360 pp. Edmonton, Univ. Alberta Press. (Transl. from *Trudȳ paleont. Inst.*, Moscow, **100**. 311 pp. 1964).

Schlee, H. B. & Schlee, D. 1976. Bibliographie der rezenten und fossilen Mecoptera. *Stuttg. Beitr. Naturk.* (A) **282:** 1–76.

Scudder, S. H. 1886. A review of Mesozoic Cockroaches. *Mem. Boston Soc. nat. Hist.* **3:** 439–485.

—— 1890. *The Fossil Insects of North America, with notes on European species*, **1** (Pretertiary). 455 pp., 35 pls. New York.

Seward, A. C. 1904. *Catalogue of the Mesozoic plants in the Department of Geology, British Museum* (*Natural History*). The Jurassic Flora, II. Lias and Oolitic Floras of England. 192 pp., 13 pls. London.

Sharov, A. G. 1968. [Phylogeny of the Orthopteroidea]. *Trudȳ paleont. Inst.*, Moscow, **118**. 217 pp., 12 pls (In Russian; transl. 1971 Israel Progr. Sci. Transls, Jerusalem. 251 pp. incl. pls).

Tillyard, R. J. 1922. The Mesozoic insects of Queensland, 9. *Proc. Linn. Soc. N.S.W.*, Sydney, **47:** 447–470.

—— 1925. The British Liassic Dragonflies (Odonata). *Fossil Insects* **1**. 40 pp., 5 pls. London, British Museum (Natural History).

—— 1933. The Panorpoid complex in the British Rhætic and Lias. *Fossil Insects* **3**. 79 pp., 1 pl. London, British Museum (Natural History).

—— 1935. The evolution of the Scorpionflies and their derivatives (Order Mecoptera). *Ann. ent. Soc. Am.*, Washington, **28:** 1–45.

—— **& Fraser, F. C.** 1938–40. A reclassification of the Order Odonata. *Aust. Zool.*, Sydney, **9:** 125–169, 195–221, 359–396.

Tindale, N. B. 1980. Origin of the Lepidoptera with description of a new mid-Triassic species and notes on the origin of the Butterfly stem. *J. Lepid. Soc.*, Cambridge, Mass., **34** (3): 263–285.

Tjeder, B. 1966. Neuroptera Planipennia. 5. Family Chrysopidae. *S. Afr. anim. Life*, Stockholm, **12:** 228–534.

Vishnyakova, V. N. 1964. Osobennosti zhilkovania perednikh krȳl'ev novogo pozdneyurskogo tarakana [Peculiarities of the venation in the forewings of a new Late Jurassic cockroach]. *Paleont. Zh.*, Moscow, **1964** (1): 82–87 (In Russian; Engl. transl. 1965, *Int. Geol. Rev.*, Washington, 7 (8): 1456–1460).

—— 1968. Mezozoĭskie tarakanȳ s naruzhnȳm yaĭtsekladom i osobennosti ikh razmnozheniya (Blattodea) [Mesozoic cockroaches with external ovipositor and features of their reproduction]. *In* Rohdendorf 1968 (q.v.): 55–86, pls 6–8.

Westwood, J. O. 1845. (see Brodie).

—— 1849. *In* Brodie, P. B., Notice on the Discovery of a Dragon-fly and a species of *Leptolepis* in the Upper Lias near Cheltenham, with a few remarks on that formation in Gloucestershire. *Q. Jl geol. Soc. Lond.* **5** (3): 31–37.

Whalley, P. E. S. 1978. New taxa of fossil and Recent Micropterigidae with a discussion of their evolution and a comment on the evolution of the Lepidoptera. *Ann. Transv. Mus.*, Pretoria, **31:** 71–86.

—— 1982. *Bintoniella brodiei* Handlirsch (Orthoptera) from the Lower Lias of the English Channel, with a review of British bintoniellid fossils. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **36** (2): 143–149.

—— 1983. A survey of Recent and fossil Cicadas (Insecta, Hemiptera–Homoptera) in Britain. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **37** (3): 139–147.

—— **& Jarzembowski, E. A.** 1985. Fossil insects from the Lithographic Limestone of Montsech (late Jurassic–early Cretaceous), Lérida Province, Spain. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **38** (5): 381–412.

Willmann, R. 1978. Mecoptera (Insecta, Holometabola). *Fossilium Catalogus, Animalia*, The Hague, **124**. 139 pp.

Ziegler, P. A. 1982. *Geological Atlas of Western and Central Europe*. 130 pp., 40 pls. Amsterdam & New York, Shell Internationale P.M.B.V.

Zeuner, F. E. 1937. Description of new genera and species of fossil Saltatoria (Orthoptera). *Proc. R. ent. Soc. Lond.* (B) **6:** 154–159.

—— 1939. *Fossil Orthoptera Ensifera*. 321 pp., atlas 80 pls. London, British Museum (Natural History).

—— 1942. The Locustopsidae and the phylogeny of the Acridoidea (Orthoptera). *Proc. R. ent. Soc. Lond.* (B) **11:** 1–19.

—— 1962. Fossil insects from the Lower Lias of Charmouth, Dorset. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **7** (5): 155–171, pls 24–27.

Index

New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

Adephaga 173
Aerophasma 140
Aerophasmatidae 112, **137**
Aeroplanidae 140
Agrion buckmanni 126
Agriotes 166
ammonites 108, 110, 122, 123*, 130, 133*, 148, 149*, 157, 179, 181, 183
Amphientomidae 162
Amphiesmenoptera 159, 163
Amsurgus lateralis 136
angiosperms 163–4, 181
Anisoptera 117–18
Anisozygoptera 117, **119**, 184
Apperley 165
Annulipalpia 163
Archaegryllodes stormbergensis 135
Archaeolepidae fam. nov. 159, 163
Archaeolepis 109, 111, **159**, 163–4, 180, 183
  mane 111, **160***, 161–2
Archegocimicidae 143, 144*
Archelcana 111, **127**
  britannica 127–8
  durnovaria 111, **127***
  shurabica 129
Archidermaptera 116
Archizygoptera 117
Archithemistidae 124
Armorican massif 182
Asteroceras obtusum 122
Aust 176
Baissoptera 148
Baissopteridae 148
beetles 108, 110–11, 113, **164**, 179, 181, 184
Belstomatidae 112, 144*, **146**, 180, 184
Bennettitales 181
Bibionomorpha 113, **158**
Binton 135, 155
Bintoniellidae 112, 183
Birchi nodules 110, 130, 135, 162, 183
birds 119
Blattidae 113
Blattodea 109–10, **113**, 164, 182
Blattula 114
Brevicula 110, **116**

  gradus 110, **117**, 118*
Bristol Museum and Art Gallery 108, 143, 146
British Geological Survey 108, 148
Bucklandi Zone 183
Buprestidae 113, 173
bush-cricket 112, 181
Byrrhoidea 111, **169**, 171*

Caelifera 136
Carabidae 111, **169***, 170*, 171*
Carboniferous (Upper) 119, 127
China 182
Chresmodidae 140
Chrysopidae 149
cicada 112, 184
Cicadellidea 111, **141**, 142*
Cicadidae 140
Cicadidea 141
Cicadoprosbole 141
Cimicomorpha 143
Cixiidae 112, **143**
click-beetles 113
cockroaches 110–11, **113**, 114, 115*
Coleoptera 108–9, 111, 113, 159, **164**, 170, 172*, 174*, 180–2
Coniferales 181
Coope, R. 108
Corduliinae 126
Corixidae 111, **146**
Cornubian massif 182–3
Cretaceous 113, 127, 140, 150, 159, 163, 170, 181, 183–4
Cretophasmatidae 140
cricket 112, **126**, 181, 184
crinoids 108
Cupedidae 166
Curculionidae 111, **169**, 172*
Curculionoidea 169
Cycadales 181

degagement 110
deposition 179
Dermaptera 109–10, 112, **116**, 182
Desmatini 165
Diadocidia 158
Diastatommites liassina 125
Diptera 108–9, 111, 148, 150, 155, **157**, 159, 162–3, 181–2
Ditomyia 158
Dobbertin 182
Dolling, W. R. 109, 112, 143
Dorsettia 111, **124**
  laeta 111, 124, **125***
dragonfly 112, **117**, 181, 184
Dryopoidea 111, **169**, 171*, 172*
Dumbleton 135
Durnovaria 111, **137**
  parallela 111, **137**, 139*, 140*

earwig 112, **116**, 118*
Elater socius 165
Elateridae 113, **164**, 165, 184
Elaterina liassica 110–11, **164**
Elaterophanes 111, **165**
  regius 111, **165***
  socius 165
  vetustus 165
Elcana 127, 129
  britannica 127
  tessellata 129
Elcanidae **127**, 182
English channel 182
Ensifera 127
Eolepidopterigidae 163
Eolepidopterigina 163
Eolepidopterix jurassica 163
Ephemeroptera 111, 180, 182
Epiophlebia 117, 119, 121
Epiophleboidea 119
Eumecoptera 150, **151**
extra-floral nectaries 164

Fennah, R. G. 143
Ferganopterus 130
ferns 183
Feronia 173
Filicales 181
fish 108, 110, 164
flora 181, 183
flotation 180–1
Fraser, F. C. 124
Fulgoridea 143
fungus damage 180
fungus-gnat 113, **158**
Fungivoridea 158

Germany 112
Glossata 163
Gloucestershire 119, 130, 135, 153, 165, 176, 179
grasshoppers 126
Gryllidae 130, **133**, 182
Gryllidea 130
gymnosperms 183

Hagla gracilis 111, **130**
Haglidae 130
Harpalus schlotheimi 173, 176
Hemiphlebia 117
Hemiptera 108–11, **140**, 182
Heterobathmiina 163
Heterophlebia 111, **126**
Heterophlebiidae 126
Heterophleboidea 119
Heteroptera 108–12, **143**, 180–2, 184
  aquatic 143
Hettangian 183
Hill, C. R. 183
Holcoelytrum 173
  schlotheimi 173
  giebeli 176
Holcoptera 111, 113, **173**
  confluens 176
  giebeli 111, 175*, **176**, 177*, 178*
  schlotheimi 111, **173**, 175*
Homoptera 109, 112, **140**, 181–2
Homopterites 140
Hymenoptera 109, 111, 182
Hypnomorphini 165–6
Hypsothemis 111, **123**
  fraseri 111, **124***
  jurassica 124

Incurvariidae 159
Institute of Palaeontology, Moscow 109
Integripalpia 163
intraspecific variation 114

Jackson, J. F. 108
Jarzembowski, E. A. J. 180, 183
Julodis 113, 173
Jurassic sea 176

Karataogryllus gryllotalpiformis 132
Karatau 137, 156, 182
Kazakhstan 116
Kimochrysa 149

land-mass 182–3
larvae 111, 163–4
Lepidoptera 109, 111, 113, 150, **159**, 163, 182
Lepidopsocidae 162
Leptopodomorpha 144*, 145
Lestomorpha 119
Liassocupes 111, **166**
  giganteus 111, **167**, 169*
  maculatus 111, **167**, 168*
  parvus 111, 166*, **167**
Liassogomphus 119
Liassophlebia 110–11, **120**
  anglicanopsis 111, **122**, 123*, 179
  gigantea 111, **122***
  jacksoni 110, **121***
  magnifica 120–1
  pseudomagnifica 110, **120***
Liassophlebiidae 119
Libellulomorpha 119
Locustopsidae 136
Locustopsidea 136
Locustopsis **111**, 136
  elegans 136
  spectabilis 111–12, **137**, 138*
London–Brabant massif 182

mangrove swamp 176, 179
Mantidae 129
Margaroptilon 140
Mecoptera 108–9, 111–12, **150**, 162, 181–2
Meganisoptera 117
Melyridae 173
Mesoblattina geikiei 116
Mesoblattinidae 113, **114**
Mesoblattininae 113, **114**

Mesocixiella 111, **143**
  asiatica 143
  fennahi **143**, 144*
Mesonepa primordialis 111, **146**
Mesoraphiididae 147
Metaraphidia 111, **147**
  confusa 111, 147*, **148**, 149*
Micromacula 111, **135**
  gracilis 111, **135**, 136*
Micropterigidae 159, 163–4
Moscow 109
moth 159, **160**, 164
Mycetophilidae 158

Nannoblattina 110, **114**
  petulantia 110, **114**, 115*
  prestwichi 114
Necrophasmatidae 140
Nematocera 158
Nepomorpha 146
Neuroptera 108, 111, 114, 149, 181–2

Obtusum Zone 109, 114, 130, 135, 155, **179**, 183
Odonata 109–10, 112, **117**, 126, 181–2
Oedischiidea 127, 130
Omma cf. *liassica* 173, 174*
Orichalcum 111, **129**
  ornatum 111, **129**, 130*, 134*
Orthophlebia 111, **152**
  anglicus 153
  capillata 111, 150*, 151*, **152**, 154*
  communis 152
  gigantea 153
  grandis 153
Orthophlebiidae 110, 112, **151**, 162, 179–81
Orthoptera 109–12, **126**, 139, 164, 179, 181–3

Pachymeridium 145
Pachymeriidae 143, **145**
Palaeozoic 119
Panorpoid complex 108
Parasprosbole 111, **141**
  rotruda 111, **141**, 142*
Paratrichoptera 155–6
Pentatomorpha 145
Permagrion 119
Permopsocus 162
Petrophlebia **122**, 179
  anglicanopsis 122
Phasmatidae 140
Phasmatodea 109, 111–12, **137**
Phryganidium perlaeformis 155
Planorbis Zone 112, 114, 155, 179, 183
Plecoptera 182
pollen-feeding 164
Polyphaga 173
Popov, Y. A. 109, 143
Priscaenigma 148
  obtusa 147*, **148**, 149*
Prodocidia 111, **158**
  spectra 111, 154*, **158**, 159*
Protanisoptera 117
Protodiplatidae 116
Protogryllus 111–12, **133**
  dobbertinensis 133
  magnus 111–12, 134*, **135**
Protohagia 111–12, **133**
  langi 111–12, **133**, 134*
Protomecoptera 150
Protorthophlebia 111, **153**
  latipennis 111, **153***, 154*
Protozygoptera 117
Pseudopolycentropodidae 113, **155**, 162
Pseudopolycentropus 111, **155**
  latipennis 156
  prolatipennis 111, **155**, 156*, 157*
Psocoptera 159, **162**, 182
Psychoda surcoufi 163
Pterinoblattina intermixta 113
pterosaurs 119
Purbecks 111, 115, 129

Raphidioptera 108–9, 112, **147**, 157, 182
Regiata 111, **131**, 184
  scutra 111, **131***, 132*, 133*, 184
Rhaetic 173, 176, 179
Rhipidoblattina 110, 114, **116**

Sabatinca 163
Saltatoria 139*
sawfly 109
Saxony 181–2
sexual dimorphism 114, **126**
Sharov, A. G. 126
Shuraboprosbole 141
Sinemurian 109–10, 182–3
snakefly 108, **147**
sound production 112, 130
stick-insect **137**, 140
Strensham 137, 176
Symmerus 158

Taldycupedidae 167
Tenebrio 173
Tettigarctidae 111–12, 140, **141**, 184
thyridium 155
Thysanoptera 182
Toarcian transgression 183
Trias 113, 129–30, 135–6, 140, 150–3, 158–9, 163, 167, 173
Triassomantidae 129
Trichoptera 111, 155, 159, 162, **163**, 180, 182
Trigonidiinae 136
Turneri Zone 110, 130, 135, 183

ultra-violet light 110
United States National Museum 176

Warwickshire 137, 153, 173, 179, 181
waterbug 108, 112, 179, 183–4
water-logging 179
weevil 169–70
Wealden 181
Welsh-high massif 182
Western approaches 182
Worcestershire 135, 137, 176, 179, 181

Xiphopteridae 140
Xiphopteridea 137

Yorkshire Museum 176

Zeugloptera 163
zonation 109–10
Zygoptera 117–18

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The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

B. G. Gardiner

There are some 25,000 species of actinopterygians, far out-numbering the tetrapods and accounting for over half of all the living species of vertebrates. The Actinopterygii contain such diverse forms as polypterids, sturgeons, paddle fishes, gars, the bowfin and the enormous variety of teleosts. The Devonian actinopterygians described in this monograph stand near the base of the Osteichthyes, a natural group including the coelacanths, lungfishes and tetrapods.

This unique Upper Devonian fish fauna was discovered in 1963 by Mr Harry Toombs of the British Museum (Natural History) while on a collecting trip to Australia. The majority of the material was subsequently collected in 1967 by a joint expedition from the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow.

The discovery of these superbly preserved Devonian palaeoniscids at Gogo, Western Australia, has not only greatly increased our knowledge of the early actinopterygian condition but has also enabled us to appreciate the original osteichthyan plan. In other words, many of the characters of the Gogo palaeoniscids are primitive for all bony fishes, and this in turn allows comparison with the other gnathostome groups. These Devonian species also provide detailed information which illuminates many problems in the structure and evolution of the actinopterygians. This knowledge has permitted a more comprehensive and soundly based account of the history of that group.

The relationships are expressed in a new classification of gnathostomes in which the placoderms are considered to be the sister-group of the osteichthyans, the acanthodians the sister-group of those two and the chondrichthyans the primitive sister-group of other gnathostomes. The Porolepiformes are considered to be the sister-group of the choanates.

Finally the interrelationships of actinopterygians are reviewed and the great range of fossil forms presently included in the Palaeonisciformes discussed.

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By J. J. Hooker

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Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England

J. J. Hooker

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Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England

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Contents

Synopsis 192
Introduction 192
Materials and methods 193
Collecting 193
Curation of small teeth 194
Measurements 194
Photographic work 194
Taxonomic procedure 195
Abbreviations 195
Institutions and collections 195
Teeth 195
Other 197
Localities and stratigraphy 197
Elmore, Hampshire 197
Hengistbury, Dorset 199
Barton Cliff, Hampshire 199
Introduction 199
Lithostratigraphy of the 'Barton Beds' – historical background 199
Lithostratigraphy of the 'Barton Beds' – interpretation 200
Formal designation of the Barton Clay Formation 203
Formal designation of the Becton Sand Formation 205
Sands above the 'Hengistbury Beds' 206
Discussion of B.G.S. concept 206
Cyclothems in Christchurch Bay 206
Creechbarrow, Dorset 207
The succession near the summit 207
The Creechbarrow Limestone Formation 209
Interpretation of bed 12 210
Beds 1–11 210
The superficial deposits 211
Structure 212
Systematic palaeontology (see Table 1, pp. 212–215) 212
Correlation 415
Range of the Bartonian in England 415
Concepts of the stage 415
The lower limit of the Auversian in England 416
The upper limit of the Marinesian in England 417
The Auversian–Marinesian boundary in England 417
Radiometric dates 418
Mammal correlation in the Bartonian 418
Introduction 418
Creechbarrow 419
Range of Bartonian mammalian taxa and definition of zones 420
i. The *Palaeotherium eocaenum–Lophiodon rhinocerodes* Concurrent Range Zone 420

Bull. Br. Mus. nat. Hist. (Geol.) **39** (4): 191–478

Issued 27 March 1986

- ii. The *Lophiodon lautricense–Lophiotherium siderolithicum* Concurrent Range Zone ... 420
- iii. Discussion ... 424
- iv. Further subdivision by mammalian biostratigraphy ... 425
- Evidence from Hampshire Basin sedimentation ... 429
- Palaeoenvironments, palaeoecology and palaeogeography ... 430
  - Depositional environments ... 430
    - The marine province ... 430
    - The non-marine province ... 432
      - i. Notes on aspects of the biota ... 433
      - ii. Problem of distinction of stromatolites from calcretes ... 436
      - iii. Conclusions ... 436
    - Tectonic hypothesis ... 437
  - Palaeoecology of the Creechbarrow mammal fauna ... 438
    - Introduction ... 438
    - Preservation ... 438
    - Faunal composition ... 440
    - Notes on diet, habits and habitat ... 442
  - Conclusions ... 447
  - Palaeogeography ... 448
    - Faunal provinces ... 448
    - Migrations after the Bartonian ... 450
- Acknowledgements ... 450
- References ... 451
- Index ... 472

Synopsis

The lithostratigraphy of deposits laid down during the Bartonian in the Hampshire Basin is described. The new formal terms Barton Clay Formation and Becton Sand Formation are defined. The Elmore Formation is reduced to member rank within the Barton Clay Formation. A pattern of cyclic sedimentation within the Barton Clay Formation, Becton Sand Formation and part of the Boscombe Sands is recognized.

Fifty-three mammalian taxa of species group rank, represented mainly by teeth but also by some important cranial and postcranial elements, are described from the Creechbarrow Limestone and Barton Clay Formations. Of these, 12 are new: *Gesneropithex figularis*, *Nannopithex quaylei*, *Microchoerus wardi*, *M. creechbarrowensis*, *Europolemur collinsonae*, *Plesiarctomys curranti*, *Sciuroides rissonei*, *Suevosciurus authodon*, *Heterohyus morinionensis*, *Vulpavoides cooperi*, *Plagiolophus curtisi* and *Haplobunodon venatorum*. *Plagiolophus curtisi* is divided into two subspecies, the nominate one and *P. curtisi creechensis*. *Treposciurus helveticus* is here raised from subspecific rank and a new subspecies, *T. h. preecei*, is added. Some species formerly placed in *Anchomomys* (order Primates) are included in *Gesneropithex* (order Lipotyphla). The contents of the family Pseudosciuridae and of the genera *Cebochoerus* and *Acotherulum* are revised. Genus records from Creechbarrow are the earliest for *Treposciurus* and *Suevosciurus* and the latest for *Nannopithex*, *Europolemur* and *Vulpavoides*. Of the named taxa, 11 of the genera and all except three of the species are new records for the English Palaeogene.

Biostratigraphic correlation within the Bartonian of Europe, especially that by means of mammals, is discussed. Two mammalian concurrent range biozones, spanning the late Lutetian and Bartonian, are defined. Correlation from the non-marine to marine facies is attempted by integrating the mammal data with those from other organisms.

Tentative conclusions are drawn concerning depositional environments; mammalian palaeoecology is discussed for the Creechbarrow locality. Some aspects of palaeogeography are considered for the European Bartonian.

Introduction

Land mammals have long been known from Ludian deposits of the Hampshire Basin (e.g. Wood 1846) and have been the subject of some recent studies (e.g. Bosma 1974, Cray 1973, Insole 1972). They are much scarcer in the underlying marine Barton Clay and the discovery of several specimens by amateur geologists at Barton Cliff was a matter of interest (Hooker 1972). However, the small number of specimens and the unlikelihood of any more coming to light seemed to preclude further studies. An independent investigation of the equivocally dated non-marine Creechbarrow Limestone, launched in 1975, led to the discovery of a rich mammalian fauna of Bartonian age (Hooker 1977*b*). The small number of mainland European Bartonian mammal sites makes this fauna important on a continental scale. The pioneers of Creechbarrow geology, Hudleston (1902*a*, 1902*b*, 1903) and Keeping (1910, 1912), made large excavations, but without undertaking any sieving of the sediment. In recent decades sieving has come to the fore as a field technique (e.g. Kühne 1969, McKenna 1962, Insole 1972), and the rich fauna described here was retrieved solely by this means.

It was decided to undertake a detailed taxonomic treatment of all the available English Bartonian mammals, which are known only from the Hampshire Basin. Some basic lithostratigraphic classification was found to be necessary for much of the sequence of strata, because of the mixed nature of earlier stratigraphic studies and the recent indiscriminate application of formal lithostratigraphic rank terms to non-lithostratigraphic or undefined units.

The presence of land mammals in the marine as well as the fresh-water facies of the Hampshire Basin suggested the possibility of biostratigraphic correlation across this otherwise difficult environmental boundary. A possible reconciliation of some of the discrepancies between current mammalian and marine invertebrate zonal and dating schemes in Europe was thus envisaged. A brief interpretation of the environments and mammalian palaeoecology and palaeobiogeography was also considered a useful corollary and to make the study as comprehensive as possible.

Materials and methods

Collecting

Collecting by the author and his colleagues was restricted to the Creechbarrow locality. Material from other localities was mainly the result of collecting by enthusiastic and competent amateur geologists.

The first attempt at excavation of the Creechbarrow Limestone at Creechbarrow was carried out on a Tertiary Research Group field meeting from 19–20 July 1975. Trench excavation was begun on the east side of the hill just below the summit, but had to be abandoned because of the amount of hillwash and talus, probably from old excavations. A second excavation (Hole 1) was opened higher and immediately east of the summit trigonometrical point. In this hole, below the soil layers, marl and rotted limestone were found and 27 kg were removed. This sample yielded the first remains of mammals since Keeping's work (1912). Hole 1 was widened and deepened on 2 August 1975 to become Hole 2 (subsequently considered together with Hole 1) and 282 kg of matrix were removed. Hole 3 was dug on 6–7 December 1975 and 840 kg were removed. More intensive excavation work funded by the British Museum (Natural History) (BM(NH)) was carried out from 30 May–4 June 1976 and resulted in the removal of 4190 kg of matrix from Holes 4 and 5. A further BM(NH) excavation from 28 July–12 August 1978 resulted in Holes 6 and 7, about 5700 kg being removed from Hole 6.

Matrix from Holes 1–5 was removed entire for laboratory processing. Most of that from Hole 6 was initially wet-sieved in a nearby flooded quarry, using an Alcon water pump and a stack of sieves ranging in mesh size from 10 mm to 0·5 mm. The concentrate was then transported back to the BM(NH). A map of the holes is shown in Text-fig. 4, p. 209.

The present report covers material recovered by complete processing of the marl matrix from Holes 1–3 and part of Hole 4 (bags 1–36); and initial coarse processing for larger, rarer species from the rest of Hole 4 and Holes 5–6. Matrix processed in the laboratory was first allowed to dry, weighed and allowed to break down in hot water before being sieved through 0·5 mm mesh size. The residue was dried and graded above and below 4 mm mesh. The dried fraction >4 mm was then sorted for fossils. The 0·5–4 mm fraction was treated with dilute acetic acid to remove the limestone fragments. The insoluble residue was washed of acid salts, dried and graded above and below 1 mm mesh for greater ease of sorting. In a trial sample of the lower size fraction, nothing but a few bone fragments was found. Although all of this size fraction was retained for further concentration in the future, only that above 1 mm was sorted further for vertebrates and any other fossils that had survived the acid treatment. This fraction was found to be rich in mammals, at a concentration of about one tooth per kilogram of unprocessed matrix (dry weight). The inorganic insoluble residue in the acid-treated samples is mainly angular to subangular quartz sand.

All the material collected is in the Department of Palaeontology, British Museum (Natural History) and the distribution of numbered mammalian specimens per excavation hole is recorded below.

Holes 1/2: M35390–444, M35446–599, M36499, M36790–829, M36860.
Hole 3: M35600–6259, M36380–447, M36497–8, M36500.
Holes 4–5: M35445, M37090–571.
Hole 6: M37690–719.

Specimens already in museum collections are listed below. The BM(NH) cast number follows in brackets those in other museums, where relevant.

Barton: M11090, M12346, M26176, M26238, M26552–3, M26649, M29090–1, M34864–5.
Elmore: M36491, GM.978110–1 (M36493), GM.978110–2 (M36492), GM.978110–3 (M41977).
Hengistbury: IGS. GSM88617 (M31996).
Creechbarrow: SMC. C9968 and C9969 (M33501).

Curation of small teeth

The small teeth were all mounted on stainless steel entomological pins, inserted in corks, which were in turn inserted into flat-bottomed glass tubes. This allowed the register number to be written on an object (the cork) actually attached to each specimen, as well as on the glass tube, and should minimize long-term loss or muddling of specimens through study.

Measurements

The larger specimens were measured using an 8-inch Mitutoyo vernier caliper. Smaller specimens in the BM(NH) were measured using a calibrated micrometer eyepiece in a Nikon SMZ-10 binocular microscope; similarly calibrated micrometer eyepieces on a variety of binocular microscopes were used in other institutions.

The main tooth measurements are:

Maximum mesiodistal dimension (l);
Maximum buccolingual dimension (w);
Maximum buccolingual dimension of trigonid of lower molariform teeth (w_1);
Maximum buccolingual dimension of talonid of lower molariform teeth (w_2).

Thus in the case of incisors, e.g. of rodents, the mesiodistal dimension is in fact in a mediolateral direction and the buccolingual dimension in an anteroposterior direction. Where problems arise and/or exceptional parameters are used, this is discussed in the text. The standard deviation (s) and coefficient of variation (v) are calculated according to the methods of Simpson *et al.* (1960).

Photographic work

Pl. 35, fig. 1c (p. 434) was taken on a Leitz Ortholux II. Most of the other light macrographs were taken using a Zeiss Tessovar or a Leitz Aristophot. In nearly every case, the specimens were first coated with ammonium chloride to overcome the confusing effects of shine on tooth enamel and of preservational colour. The scanning electron micrographs (SEM) were taken using an ISI Stereoscan 60A. The specimens for scanning electron microscopy were cleaned with acetone, mounted on aluminium stubs using Durofix and photographed at 2 kv without coating. Absence of coating and use of Durofix as a mounting medium meant that the specimens could be easily returned to their normal storage without the tedious task of removing the coating. Teeth are figured as from the left side, i.e. figures of right teeth are shown reversed in nearly every case.

Taxonomic procedure

For each taxon in the systematic section (pp. 212–415), except where identification is only at a high taxonomic level, a diagnosis (new or emended) or a reference to the most recent diagnosis is given.

Synonymy lists for genera are not intended to be comprehensive but to give a range of the names that have been applied. Those for species refer mainly to the British material under discussion. Historical accounts of wider synonymy are given where relevant. Procedure and terminology follows Matthews (1973).

Where information from the English material has allowed clarification or changes in supraspecific groupings, either a stratophenetic (e.g. *Suevosciurus*) or a cladistic (e.g. Microchoerinae) approach has been employed. The choice was dependent on the nature of the available data (see Fortey & Jefferies 1982).

The importance of size differences in cheek teeth of mammals for distinction at species level is recognized (see Gingerich 1974, 1976*a*). High coefficients of variation (i.e. *c*.8 or more) for mainly length measurements of preultimate molars with or without polymodality of the normal curve is taken to indicate more than one species. Whilst it is always impossible with fossils to be completely certain, if large numbers of specimens produce a normal curve with a low coefficient of variation and continuous range of morphological variation, it is highly probable that one is dealing with a biospecies.

If the species concept is a difficult one, the problems of relating assemblages (especially ones in close stratigraphic succession) to named species, from which they differ only slightly, or of deciding on erection of subspecies, are almost insoluble within our present system of taxonomy. A general principle has been followed that a subspecific name may be used if the difference (either morphological or size) is noticeable but less than is found between closely related species from one locality, belonging to the same or a related genus. In cases of doubt, the specific prefix 'aff.' has been used, 'cf.' being retained for uncertainty of identification on account of incompleteness.

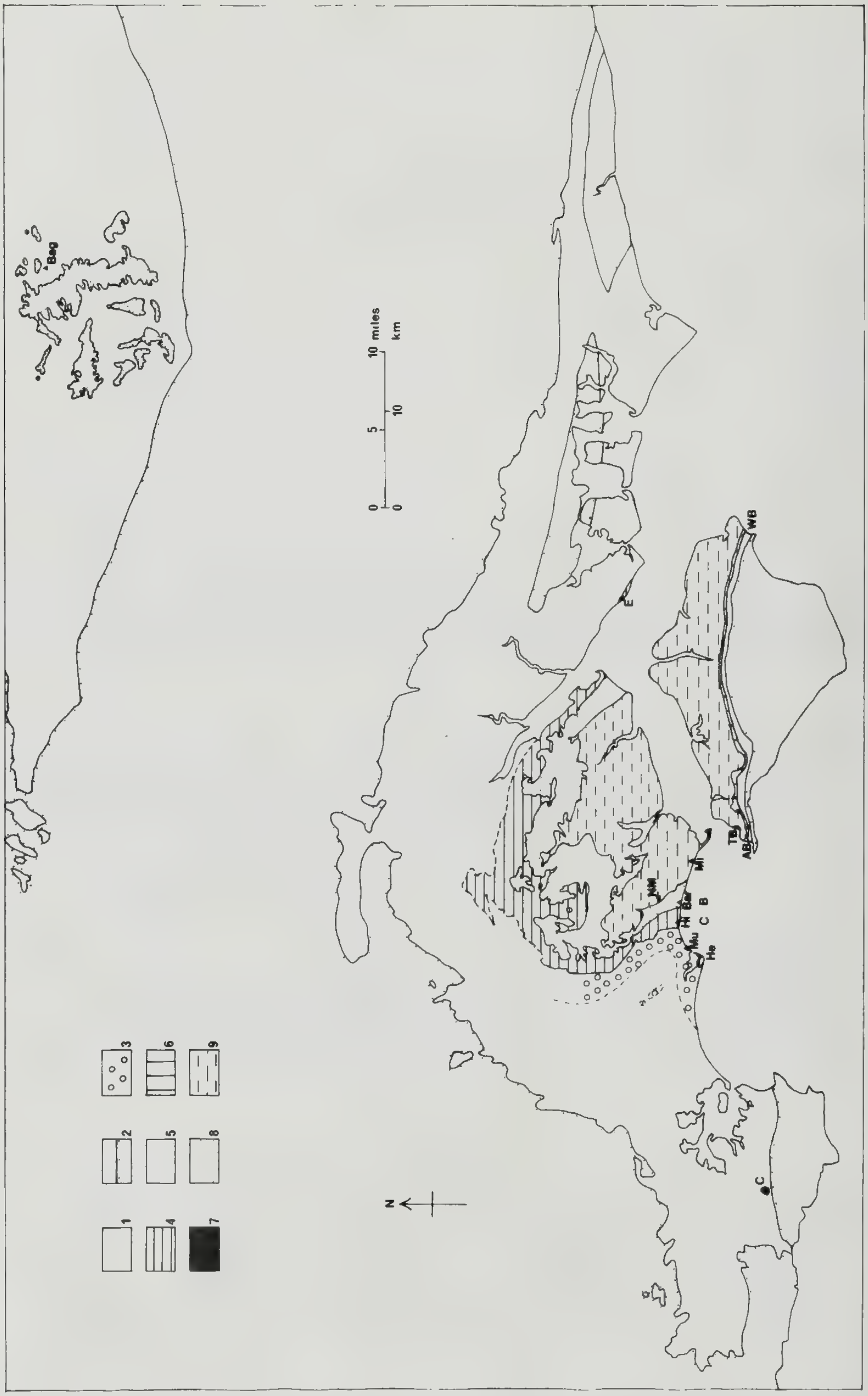
Abbreviations

Institutions and Collections. The following abbreviations are used throughout, appended to mammal specimen numbers, except that Department of Palaeontology, BM(NH), specimen numbers are not given the BM(NH) prefix: they may be recognized either by the prefix 'M' or absence of a prefix for mammalian specimens, and the prefixes GG, In, P, R and V for other biota.

BGS	British Geological Survey, Keyworth and London (formerly Institute of Geological Sciences, London).
BM(NH)	British Museum (Natural History), London.
CGH	Crochard, Girardot, Herman Collection, Brussels, Belgium.
FSL	Faculté des Sciences, Université Claude Bernard, Villeurbanne, Lyon, France.
GH	Geiseltalmuseum, Martin-Luther-Universität, Halle-Wittenberg, D.D.R.
GIU	Instituut voor Aardwetenschappen (formerly Geologisch Instituut), Rijksuniversiteit Utrecht, Netherlands.
GM	Gosport Museum, Hampshire.
IRSNB	Institut Royal des Sciences Naturelles, Brussels, Belgium.
LGM	Musée Géologique de Lausanne, Switzerland (LM = Lausanne Museum, Stehlin's numbering).
MNHN	Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France.
NMB	Naturhistorisches Museum, Basel, Switzerland.
SMC	Sedgwick Museum, Cambridge.
UM	Laboratoire de Paléontologie des Vertébrés, Université de Montpellier, France.
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, U.S.A.

Teeth

I = incisor
P = premolar
DP = deciduous premolar
DI = deciduous incisor
M = molar
C = canine
DC = deciduous canine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Other

L = left R = right

ICZN = International Commission for Zoological Nomenclature.

ISSC = International Subcommission on Stratigraphic Classification.

Localities and stratigraphy

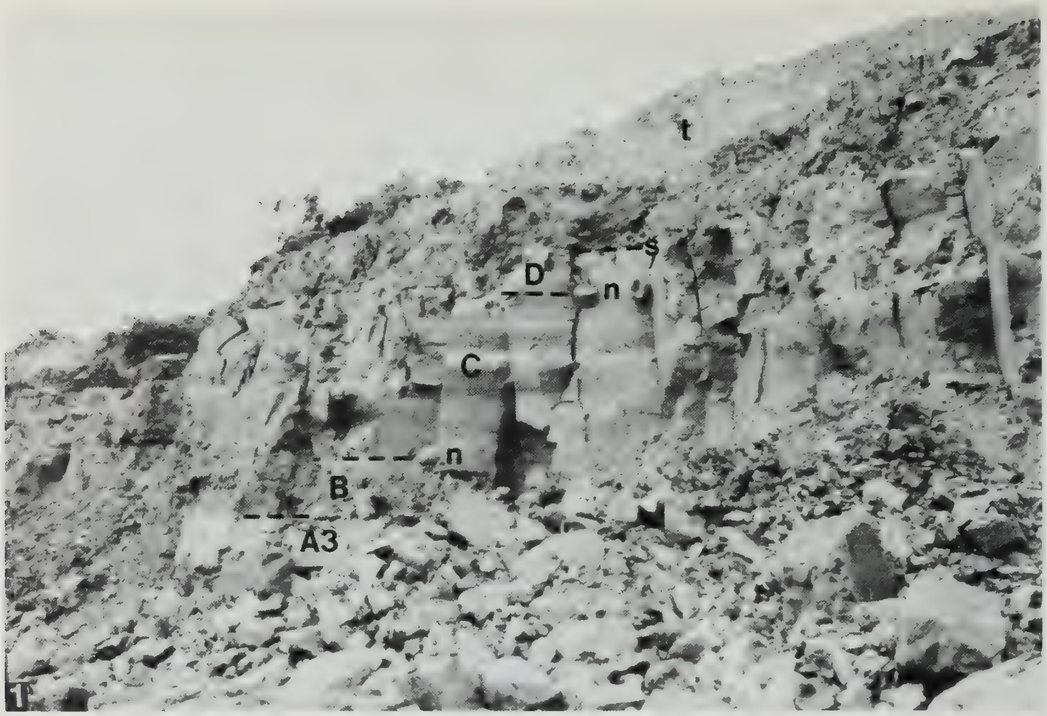
The Bartonian Stage in the concept of continental European palaeomammalogists has comprised the Auversian and Marinesian Substages and it is this period of time which is covered here. The recent restriction of the Bartonian by Curry (1981) is discussed below under correlation, p. 415. Four mammaliferous localities attributed to the Bartonian (one Auversian, three Marinesian, see correlation section) are now known in the Hampshire Basin of southern England. Text-fig. 1 shows the outcrop of Bartonian strata in the London and Hampshire Basins, i.e. upper part of Boscombe Sands; Barton Clay Formation (formally defined here for the first time); Becton Sand Formation (formally defined here for the first time); 'Upper Bagshot Beds'; and Creechbarrow Limestone Formation. Hooker & Ward (1980: tab. 1) show the whole London and Hampshire Basins sequence of vertebrate-bearing Palaeogene strata.

Elmore, Hampshire

This locality is a foreshore exposure just SE of Lee-on-the-Solent, Hampshire (National Grid Reference SU 563001 to SZ 565996). Between here and Stubbington, 3 km to the NW (SU 545018) there is a series of intermittent tidally-controlled exposures of Bracklesham Beds (Selsey and Huntingbridge divisions of Curry *et al.*, 1977). They dip at *c*.2° SW and contain a fully marine invertebrate and fish fauna (see Kemp *et al.* 1979). The strata of the Huntingbridge division at Elmore have been described in detail by Kemp *et al.*, (1979) and named the Elmore Formation. Its lithology is described as 'predominantly interbedded silty clays, clayey silts and sandy silts, usually extensively bioturbated, passing in some areas to a monotonous sequence of clayey silts .... Disseminated fine glauconite is usually present, but medium and coarse glauconite only occurs in the basal 5 m; occasional pebbles have been seen at the basal contact'. It is thus easily distinguished from the underlying 'shelly and nummulitic sandy clays and silty sands of the Selsey division' from which it is separated by a disconformity. Its top is defined by the overlying *Nummulites prestwichianus* bed, which is a biostratigraphic unit, but which is sometimes also lithologically distinctive. Apart from this marker horizon, the Elmore Formation was not clearly distinguished from the overlying Barton Clay by Kemp *et al.* (1979). It is here included as a member within the Barton Clay Formation. (See discussion below under Barton Cliff locality.)

Text-figure 1 Outcrop map of English Bartonian strata. 1 = pre-Bartonian strata. 2 = the edge of the Tertiary outcrops, with the dots outside. 3 = Boscombe Sands. 4 = Barton Clay Formation. 5 = Becton Sand Formation. 6 = Boscombe Sands, Barton Clay Formation and Becton Sand Formation undifferentiated. 7 = Creechbarrow Limestone Formation and unnamed sands below. 8 = Upper Bagshot Beds. 9 = younger Tertiary overlying Bartonian strata. The Upper Bagshot Beds outcrop in the London Basin, the remaining Bartonian and post-Bartonian strata in the Hampshire Basin. The northern edge of the mainland outcrop of the Barton Clay Formation is shown broken. Inclusion herein of the Elmore Formation (Huntingbridge division of the Bracklesham Group) within the Barton Clay Formation means that the basal boundary in this area has not yet been mapped. It is thus shown tentatively, based on information from Studley Wood, Huntingbridge, Marchwood, Dibden, Fawley and Elmore. Small solid triangles indicate towns.

Abbreviations: AB = Alum Bay; Bag = Bagshot; Bar = Barton; C = Creechbarrow; CB = Christchurch Bay; E = Elmore; He = Hengistbury; Hi = Highcliffe; Mi = Milford; Mu = Mudeford; NM = New Milton; TB = Totland Bay; WB = Whitecliff Bay. Sources of data: Reid (1898, 1902*a*, *b*) and White (1915, 1921*a*) and related one inch geological maps; Arkell (1947), Clarke (1981), Gardner *et al.* (1888) and Hooker (1975).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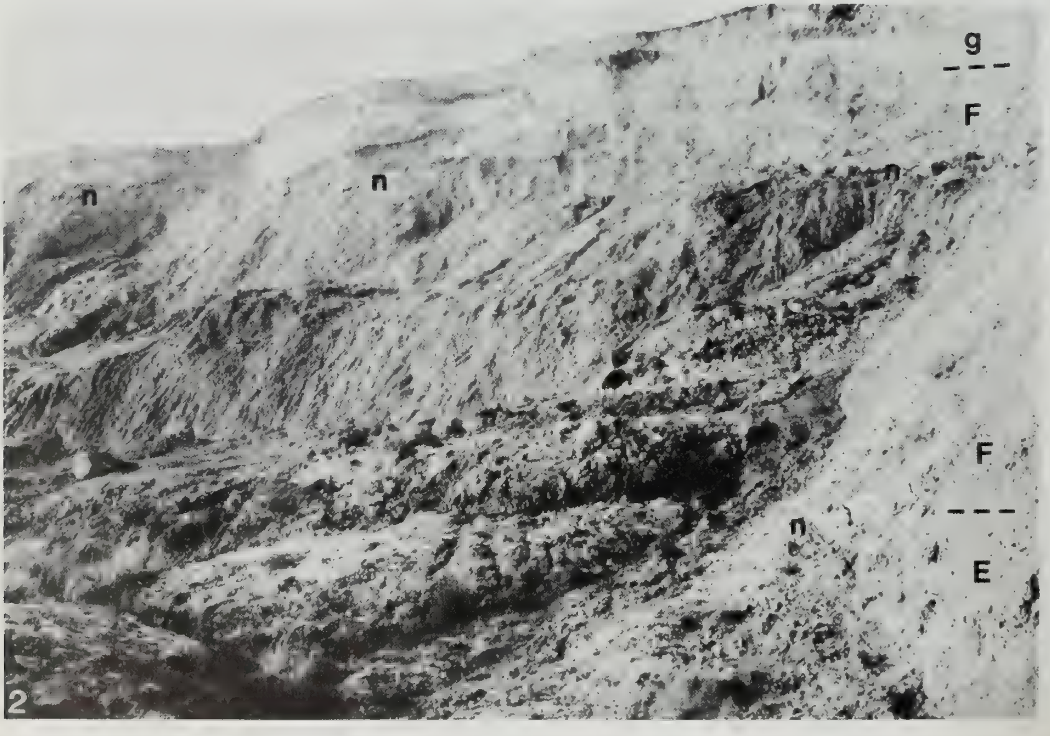
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There are only four mammalian specimens in total. They were surface-collected by Messrs D. J. Kemp and W. J. Quayle and their provenance in the lower part of the Elmore Member (all that is exposed at Elmore) is based on preservation and proximity to the outcrop, coupled with the knowledge that beach material moves little. In support of this last point, the abundant beach-collected Elmore shark fauna retains its individuality from that of Long Bank, Lee (Selsey division), less than 1 km to the NW (see Kemp *et al.* 1979: 95).

Hengistbury, Dorset

This locality is a sea cliff about 1·5 km long and a maximum of 35 m high, on a promontory known as Hengistbury Head (SZ 1790). It comprises, from below upwards: Boscombe Sands, Barton Clay Formation (formerly known as Hengistbury Beds) and unnamed sands (incorrectly called Highcliff Sands by Gardner (1879) but herein tentatively referred to the Becton Sand Formation (q.v., p. 205). Historical reviews as well as detailed sections and faunal lists were given by Hooker (1975) and Curry (1977). The only mammalian specimen from this locality is, according to preservation, from the 'Hengistbury Beds' (Hooker 1977*a*). The 'Hengistbury Beds' are sandy clayey silts to clayey silty sands with pebble beds, richly glauconitic in the lower part and with siderite nodules in the upper part, with a shallow marine invertebrate and fish fauna. They are here formally included in the Barton Clay Formation (see below under Barton Cliff locality) following Prestwich's (1849) identification, but within which they probably require separate member status. Final evidence that the 'Hengistbury Beds' are lateral equivalents of and do not dip below the Barton Clay has been provided by the Christchurch borehole (Freshney & Edwards 1983). It shows Barton Clay and the subjacent Boscombe Sands to rest directly on a thick sequence of non-glauconitic sands with interbedded clays and lignites.

Barton Cliff, Hampshire

Introduction. The sea cliffs of Christchurch Bay from Christchurch Harbour in the west to Milford-on-Sea in the east are up to 30 m high and divided into four stretches by river valleys, the steep-sided ones being locally known as bunnies. The second stretch from the west is delimited westwards by Chewton Bunny (marking also the Hampshire–Dorset border) and eastwards by Becton Bunny and is known as Barton Cliff. Barton-on-Sea is situated about midway along its length. The strata in Christchurch Bay dip fairly regularly and very gently (*c*.2°) NE. In upward stratigraphic succession are exposed: the Boscome Sands, Barton Clay Formation, Becton Sand Formation (both defined here), Lower Headon Beds and basal unit of the Middle Headon Beds. The brackish to freshwater Lower Headon Beds in this section contain a well-known early Ludian mammal fauna at Beacon and Hordle Cliffs. At least three levels in the Barton Clay, at 35 m, 40 m and 48 m below the base of the Headon Beds, contain a few important marine and terrestrial mammals (Pl. 1; Text-fig. 2; Halstead & Middleton 1972; Hooker 1972).

Lithostratigraphy of the 'Barton Beds' – Historical background (see Text-fig. 3). As recorded by Curry (1958*a*), the term 'Barton Clays' was coined by Prestwich (1847: 355) for the 'clays of Barton'. Prestwich (1846) and previous authors (see Prestwich 1846: 224–226) had considered these clays to be part of the London Clay. Although the type locality of the Barton Clay is

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Plate 1 Sections in Barton Clay Formation, Barton Cliff, Hampshire. For scale, see bed thicknesses in Text-fig. 2, p. 201.

Fig. 1 Wave-washed lowest cliff terrace between Chewton Bunny and Barton-on-Sea. Beds A3 to D are shown. Bed C is delimited by nodule bands (n) and is also marked by a central, prominent, light-coloured non-glauconitic clay band. Talus (t) moves on a slide plane (s) over the lowest part of bed D.

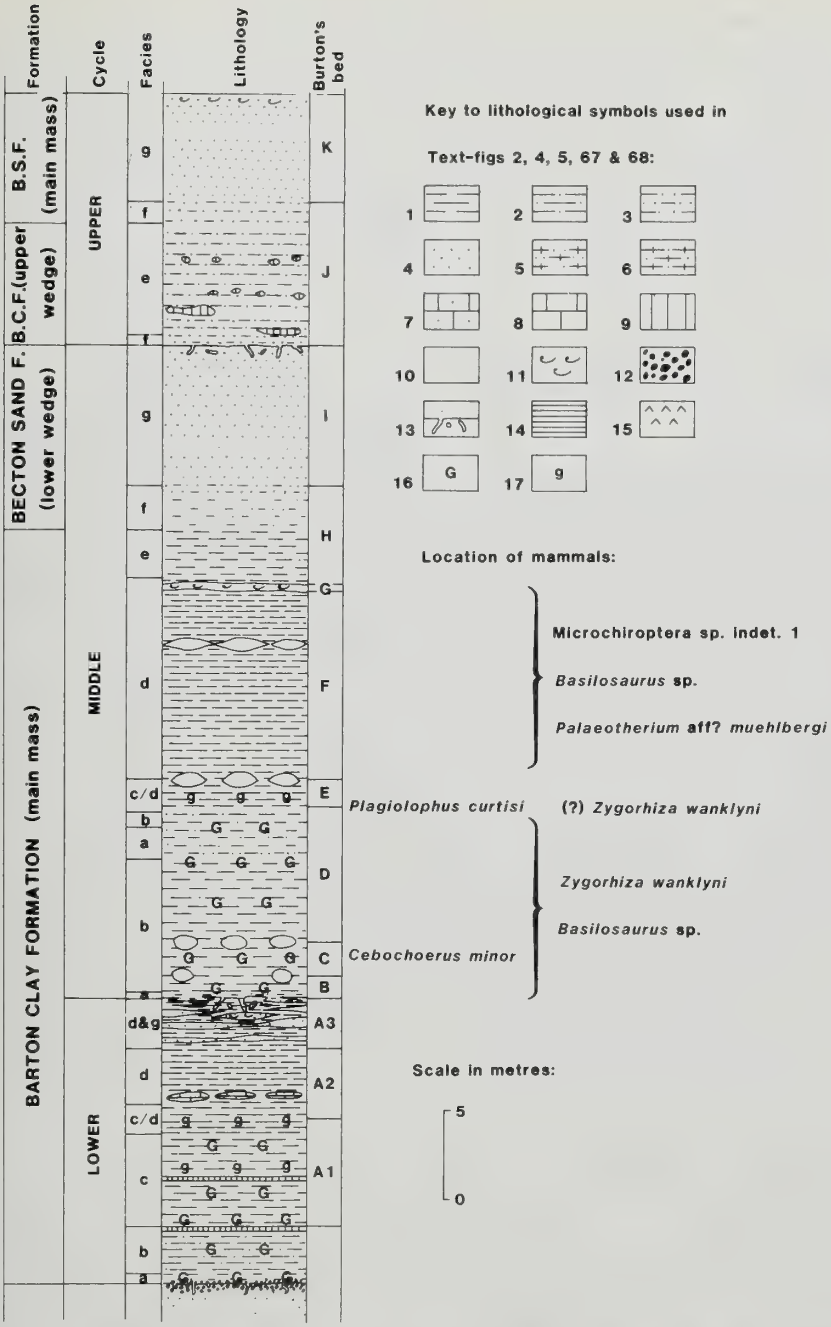
Fig. 2 Upper cliff terraces between Chewton Bunny and Barton-on-Sea. Beds E to F are shown, capped by Pleistocene plateau gravel (g). Nodule bands (n) separate beds E and F and also upper and lower parts of bed F.

Barton Cliff, most of Prestwich's attention to this stratigraphic unit was focused on Alum and Whitecliff Bays on the Isle of Wight, as these are the localities at which he had drawn up his detailed sections in 1846. At Alum Bay, Prestwich's Barton Clay is easy to define because it is sandwiched between two sand units and there is a prominent pebble bed at the base. The upper sands, termed Headon Hill Sand by Prestwich (1846: 243) are succeeded everywhere by what has long been known as the Fluvio-marine series (Prestwich 1846: 243). In Christchurch Bay, however, a bed of clay divides the upper sands into two parts. As Curry (1958*a*: 14) noted, it is not clear whether the top of the Barton Clay at the type locality is at the top of this clay bed or lower down at the top of the main mass of clay. Moreover, it does not appear that at the time Prestwich was very well aquainted with the Barton section as he did not specify this particular point. In a later work, however (Prestwich 1857: 108), it is evident that the junction was intended to be the lower of the two alternatives.

Prestwich (1857: 108) used the term 'Barton series', comprising the Barton Clay and Headon Hill Sand. Fisher (1862: 86–91) raised the base of the Barton Series in Alum Bay from the pebble bed of the original definition to the *Nummulites prestwichianus* bed, about 14 m above, relegating the strata below to the Bracklesham Beds. Keeping (1887: 71) recognized the *N. prestwichianus* bed in Whitecliff Bay. Gardner *et al.* (1888) divided the Barton Beds (= Series) into Lower, Middle and Upper on the basis of faunal changes through the sequence. The Geological Survey in mapping used the terms Barton Clay and Barton Sand, the latter to replace Headon Hill Sand (Reid 1898: 30). Burton (1929) further divided the Barton Beds into thirteen lettered beds with an additional fourteenth (L) which referred to the Lignite Bed which Gardner *et al.* (1888: 596, fig. 4) considered to commence the Headon Beds. Burton based his beds or 'horizons' on faunal content but they often coincided with distinct lithologies and their limits were defined using lithological markers such as nodule bands (e.g. see Pl. 1). Curry (1958*b*: 12) returned to Prestwich's concept of the base of the Barton Beds in Christchurch Bay, as this was 'the natural break in the succession'. No major changes were then made until Stinton (1975), in order to comply with the Stratigraphical Code of the Geological Society of London (Harland *et al.* 1972, which differs little from Hedberg, 1972, 1976) created the term Barton Formation, incorporating the Barton Beds of Prestwich plus the Lower Headon Beds.

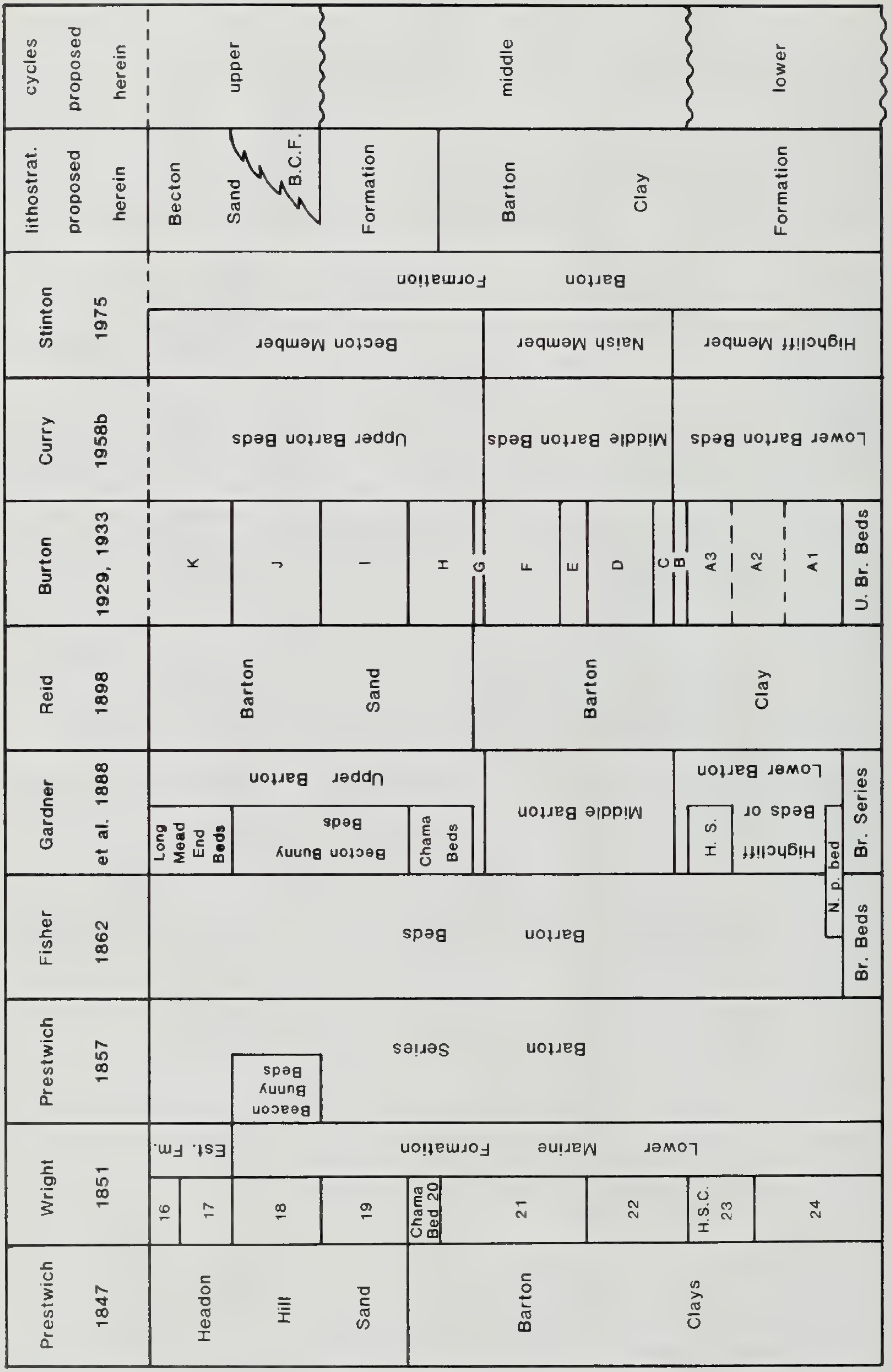
Lithostratigraphy of the 'Barton Beds' – Interpretation. Prestwich's (1847) first attempt to define the Barton Clay and Headon Hill Sand involved lithostratigraphic considerations. He ignored fauna except to show that the Barton Clay was not the same age as the London Clay. The subsequent altering of the lower limit of the Barton Clay (Fisher 1862, Keeping 1887) was based essentially on a fossil occurrence: that of *N. prestwichianus*, although Fisher also referred to lithological differences. Likewise the threefold division of Gardner *et al.* (1888) was based on biostratigraphy. Burton's system, whilst being claimed as faunal in the title of his 1933 paper, was really a composite of biostratigraphy and lithostratigraphy. Stinton's (1975) Barton Formation was stated to follow Curry (1958*a*). However, Curry (1958*a*: 14) in the section dealing with Barton Beds upheld the limits and divisions of Gardner *et al.* and Burton. Nevertheless, he used (Curry 1958*a*: 5) the term 'Bartonian Stage' (chronostratigraphy) to comprise the time of deposition of both the Barton Beds and the Lower Headon Beds (different lithostratigraphic entities), and this may be what Stinton meant. In fact, as Stinton described it, the Barton Formation coincides exactly with the Bartonian cycle of Stamp (1921: 153). Sedimentary cycles or cyclothems are stated by Hedberg (1972: 305; 1976: 36) to be informal terms for the purposes of international stratigraphy and therefore not to form the basis of lithostratigraphic terminology. The Barton Formation has therefore no lithostratigraphic foundations, nor moreover have its included members, which coincide with the biostratigraphically-based Lower, Middle and Upper divisions of the Barton Beds of Gardner *et al.*, plus the lower division of the Headon Beds. See also comments by Daley *et al.* (1979) and Stinton & Curry (1979).

The original limits of the Barton Clay and Headon Hill Sand (Prestwich 1846, 1847) correspond closely to a basic lithostratigraphic breakdown of the sequence concerned. This fact is emphasized by Curry's (1958*a*: 14) statement: 'In areas where the Barton Beds are unfossiliferous, a lithological division into Barton Clays below (corresponding roughly to the


Formation
Cycle
Facies
Lithology
Burton's bed
B.S.F. (main mass)
B.C.F.(upper wedge)
BECTON SAND F. (lower wedge)
BARTON CLAY FORMATION (main mass)
UPPER
MIDDLE
LOWER
g
f
e
f
g
f
e
d
c/d
b
a
b
a
d&g
d
c/d
c
b
a
K
J
I
H
G
F
E
D
C
B
A3
A2
A1
Key to lithological symbols used in Text-figs 2, 4, 5, 67 & 68:
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
G
17
g
Location of mammals:
Microchiroptera sp. indet. 1
Basilosaurus sp.
Palaeotherium aff? muehlbergi
Plagiolophus curtisi
(?) Zygorhiza wanklyni
Zygorhiza wanklyni
Basilosaurus sp.
Cebochoerus minor
Scale in metres:
5
0

Text-figure 2 Stratigraphical column of Barton Clay and Becton Sand Formations in Christchurch Bay. Occurrences of mammals are indicated; those on left are located with precision; those on right are located approximately according to preservation and locality data.

Key to symbols: 1, silty clay; 2, sandy silty clay; 3, clayey silty sand; 4, sand; 5, calcareous sand; 6, sandy marl; 7, sandy limestone; 8, limestone; 9, siderite; 10, 'claystone' (?phosphatic); 11, shells abundant; 12, pebbles/cobbles; 13, burrowed horizon; 14, lignitic, often laminated clay; 15, gypsum; 16, major glauconite occurrence; 17, minor glauconite occurrence.


Prestwich 1847
Headon
Hill
Sand
Barton
Clays
Wright 1851
16
17
18
19
Chama Bed 20
21
22
H.S.C. 23
24
Est. Fm.
Lower Marine Formation
Prestwich 1857
Beacon Bunny Beds
Barton Series
Fisher 1862
Barton Beds
N. p. bed
Br. Beds
Gardner et al. 1888
Long Mead End Beds
Becton Bunny Beds
Chama Beds
Upper Barton
Middle Barton
H. S.
Highcliff Beds or
Lower Barton
Br. Series
Reid 1898
Barton Sand
Barton Clay
Burton 1929, 1933
K
J
I
H
G
F
E
D
C
B
A3
A2
A1
U. Br. Beds
Curry 1958b
Upper Barton Beds
Middle Barton Beds
Lower Barton Beds
Stinton 1975
Becton Member
Naish Member
Highcliff Member
Barton Formation
lithostrat. proposed herein
Becton Sand
B.C.F.
Formation
Barton Clay Formation
cycles proposed herein
upper
middle
lower

Text-figure 3 Contrasting classifications of strata in Christchurch Bay here referred to the Barton Clay and Becton Sand Formations. Abbreviations: B.C.F. = Barton Clay Formation (upper wedge); Br. = Bracklesham; Est. Fm. = Estuary Formation; H.S. = Highcliff Sands; H.S.C. = High Cliff Sands and Clays; N.p. = *Nummulites prestwichianus*.

Lower and Middle Bartons) and Barton Sand(s) (Upper Bartons) above has been used'. White (1921*a*: 98) considered the term Headon Hill Sands to have been superseded by Barton Sand; in fact its abandonment avoids potential confusion with the Headon Beds.

In order to conform with the correct application of the procedure for international stratigraphy, it is here proposed that Barton Clay Formation and Becton Sand Formation be used for Prestwich's Barton Clays and Headon Hill Sand respectively, and that the use of the term 'Barton Formation' with its included members (Stinton 1975) be discontinued. This proposition both follows the new system and maintains as far as possible original definitions, providing mappable units which are a prime requisite of geological formations.

Formal Designation of the Barton Clay Formation

i. TERM: Barton Clay Formation.

ii. STATUS: Formal lithostratigraphic unit.

iii. STRATOTYPE LOCALITY: Cliff sections in Christchurch Bay from Friar's Cliff, Mudeford in the west to just east of Barton-on-Sea in the east.

iv. GRID REFERENCE: SZ 194927 to SZ 242927.

v. HYPOSTRATOTYPES: Cliff sections in Alum Bay (SZ 305854 to SZ 304855) and Whitecliff Bay (SZ 641862 to SZ 642863). Both show sequences more chronologically extended in Barton Clay lithology than does the stratotype.

vi. LITHOLOGY. Grey to brown silty, usually shelly (but sometimes decalcified), sometimes medium to very fine sandy, clay, with subordinate clayey sandy silts. Glauconite occurrence varies from abundant large unrolled grains to absent. The glauconitic beds contain irregular patches of very coarse subangular sand. Subsidiary beds of very fine sand also occur. There are several layers of calcareous, phosphatic and sideritic nodules. The sediments are strongly bioturbated except for the sand lithology, which is laminated and shows lenticular bedding. At the western (Hengistbury) end of the depositional basin, the sediments contain more sand and silt and less clay than at the type and most other localities. The clay mineralogy is dominantly an illite/kaolinite suite, although mainly illitic/smectitic in the Elmore facies (see Curry *et al.* 1968; Gilkes 1968, 1978; Blondeau & Pomerol 1969). Two sharp junctions occur within the formation between cyclothems (described below). Rolled flint pebbles occasionally occur through the main mass, becoming common in the extreme west, and rolled flint cobbles and/or pebbles tend to form a basal bed.

vii. BIOTA. An abundant marine invertebrate fauna, especially molluscs, and a notable shark tooth and teleost otolith fauna. Marine and land-derived tetrapods, as well as the fruits, seeds, cones and wood of land plants also occur. The most up-to-date comprehensive list is by Burton (1933). Subsequently, numerous specialist papers have appeared which include studies of organisms from the Barton Clay; these include foraminifera (Curry 1937, Murray & Wright 1974), brachiopods (Elliott 1954), molluscs (numerous papers by Wrigley; see list in Cox 1954), ostracods (Keen 1978: 439), malacostracan crustaceans (Quayle & Collins 1981, Quayle 1982), asteroids and ophiuroids (Rasmussen 1972), fish otoliths (Stinton 1975–80), sharks (Ward 1980), turtles (Moody 1980), birds (Walker 1980), marine mammals (Halstead & Middleton 1972), calcareous nannoplankton (Martini 1971, Aubry 1983), dinocysts and acritarchs (Bujak *et al.* 1980), palynomorphs (Gruas-Cavagnetto 1970), and macroplants (Chandler 1960, 1978). Some of the bivalve molluscs (e.g. *Psammotaea*) can be found in vertical life position in the sediment, whereas many other molluscs show evidence of having been buried as long dead shells colonized inside or out, or both, by bryozoans, oysters, serpulid worms and the gastropod *Capulus*, etc.

viii. THICKNESS. Approximately 40 m at Barton Cliff. It is *c.* 74 m at Alum Bay and *c.* 60 m at Whitecliff Bay. The latter is calculated at 90° to the strike; note that Gardner *et al.*'s (1888: 604) measurement of 368 ft 1 in (*c.* 112 m) for the sequence of the *N. prestwichianus* bed to the top of the Barton Sand must have been taken directly from the cliff section which is oblique to the strike. They noted that 'the section is not quite at right angles to the outcrop, and a diagonal direction may somewhat exaggerate the thickness' but apparently made insufficient allowance for this. The true measurement for this sequence is 97 m (*c.* 318 ft). The thickness at Alum Bay is probably exaggerated by tectonic disturbance (see Curry 1942: 99).

ix. RELATIONSHIPS. a. *Position of the basal junction.* The base bed of very glauconitic clayey sand to silt rests sharply, usually with a basal pebble bed, on different horizons of the light-coloured Boscombe Sands or non-marine lignitic clays in the west, and on more kaolinitic shelly sandy clays and clayey sands of the Selsey division (Bracklesham Group) (see Curry *et al.* 1968: fig. 4) in central and eastern parts of the area of deposition.

b. *Evidence.* Kemp *et al.* (1979) erected the Elmore Formation for the strata between the shelly sandy clays of the Bracklesham Beds (Selsey division) and the *N. prestwichianus* bed of the Barton Clay in Whitecliff Bay, but excluded the clays between the pebble bed and the *N. prestwichianus* bed in Alum Bay as being a different facies.

Two main problems are posed here by the Elmore as a formation. Firstly, it was described from a detailed section at Elmore, but as only the lower part was exposed at this locality, Whitecliff Bay was chosen as the type locality. Unfortunately no detailed section has ever been published of this part of the sequence in Whitecliff Bay, as it is normally vegetated in the cliff and obscured by beach material on the foreshore (see Prestwich 1846, Fisher 1862, Gardner *et al.* 1888). Recently the author had the opportunity of examining a freshly scoured exposure at the cliff foot, which showed an almost complete sequence of green, poorly glauconitic clays and silts, for about 10 m below blue clays with *Nummulites rectus.* The occurrence of *N. prestwichianus* in a richly glauconitic sand layer in the cliff, however, could not be traced to the cliff foot and may be cut out by a fault, parallel with the strike, which is visible at about the appropriate horizon (*c.* 6 m below *N. rectus* according to Curry *et al.* 1972). Nevertheless there appeared to be no change in lithology upwards from typical Elmore facies until the *N. rectus* clays were reached. Secondly, the Elmore Formation includes beds of richly glauconitic sand and sandy clay with coarse quartz grit at its base (e.g. Studley Wood and Huntingbridge). These are very similar to beds at Alum Bay and Hengistbury which were expressly excluded from the formation by Kemp *et al.* (1979), but included in Prestwich's definition of Barton Clay.

Thus the Elmore facies appears no more distinct than any of the other various minor facies which occur within the Barton Clay; and it is more appropriate to include it within the Barton Clay Formation as a member than treat it as a formation in its own right. This procedure, moreover, does not contravene historical precedent. Fisher (1862: 80) noted that 'the character of the matrix at Hunting Bridge approaches more nearly to some of the Barton deposits than to any of the Bracklesham strata'. It was only the fossils that caused him to state 'the species are so decidedly of a Bracklesham type, that I have no hesitation in classing the deposit as a part of that series'. It is easy to separate Fisher's biostratigraphy from his lithostratigraphy. Prestwich (1847) too included the upper part of the Huntingbridge division in Alum Bay in his original concept of the Barton Clay (see Fisher 1862: 87–91, and Text-figs 67–68 herein, for correlation). It seems therefore that the basal junction of the Barton Clay is successively younger when one traces it from Whitecliff Bay to Alum Bay and from there to High Cliff and Hengistbury (see Text-fig. 68 for its base at the different localities).

c. *Position of the top junction.* Where bed J is absent, the top is the transitional boundary from predominantly clay to predominantly sand within the middle cyclothem (see below); i.e. the middle of Burton's bed H, below the Chama Bed (*sensu stricto*). Where bed J is present, the top is within the upper cyclothem, the transitional boundary from predominantly clay to predominantly sand near the top of bed J. To the west (Hengistbury) the Barton Clay Formation (lower part) seems to be beginning to pass laterally into a sandy, pebbly unit, but is then truncated by modern erosion (Hooker 1975).

d. *Evidence.* In Whitecliff Bay, the upper part of the Barton Clay was called 'Chama Bed' by Gardner *et al.* (1888), in allusion to one of its shelly fossils and equivalent position in the lithological sequence to that at Barton. They noted, however, that it appeared more clayey than at the type locality. In fact, it consists of dark grey clays, becoming sandy upwards and with small tabular or irregularly ovoid siderite nodules. Its lithology thus resembles Barton bed J. It rests with a sharp junction on blue-grey sandy clays, which are correlated on dinocyst evidence (Bujak *et al.* 1980) with the sequence upper bed H–lower bed I at Barton. The best time correlations here are of the Whitecliff Bay 'Chama Bed' with Barton bed J and of the immediately underlying sandy clays in Whitecliff Bay with Barton bed I. This suggests that the sand lithology of bed I has wedged out eastwards or northeastwards. It is thus logical to include bed J at Barton in the Barton Clay Formation, despite Prestwich's (1857) decision, in view of the above evidence.

x. DISTRIBUTION: Limited by the area of outcrop in the Hampshire Basin. Main sections recorded: Barton Cliff, Alum Bay, Whitecliff Bay (Gardner *et al.* 1888), Hengistbury (Curry 1977; Hooker 1975); Studley Wood (Stinton 1970); Huntingbridge and Elmore (Kemp *et al.* 1979). Former sections: Afton, Gunville (Curry 1942), Hinton Admiral (Gardner *et al.* 1888), Bransgore, Poulner, Totton (Burton 1933), Fawley (Curry *et al.* 1968), Marchwood. Also numerous wells and boreholes (Whitaker 1910, 1917; Freshney 1978).

xi. AGE: Bartonian (Auversian plus Marinesian) to earliest Ludian?, late middle/late Eocene.

xii. SYNONYMY: Approximately equal to the Barton Clay of Prestwich (1847). Comprises Burton's (1929, 1933) beds A1 to H (lower half) and J (= Beacon Bunny Beds of Prestwich, 1857) plus the beds between the base of A1 and the pebble bed, all in Christchurch Bay. Includes Hengistbury (Head) Beds of Gardner (1879) as western unit and Elmore Formation and Huntingbridge bed(s)/division as eastern unit within the lower part of the formation. Equals the lower part of the Barton Beds/series of authors. Includes the Highcliff Sand and Clay of Wright (1851) (= A3; not the Highcliff Sand of Gardner, 1879).

Formal Designation of the Becton Sand Formation

i. TERM: Becton Sand Formation. Derived from Becton Bunny which divides Barton Cliff from Beacon Cliff and on either side of which occur the strata defined. The name is also chosen as the Formation nearly coincides with Stinton's (1975: 7) informal Becton member. Although the term Barton Sand is well known (see views of Lawson 1979), the concept of a formation distinct from the Barton Clay is considered to be best achieved by avoiding name repetition. The concept of the Barton Beds as a whole is non-lithostratigraphic and requires other definitions.

ii. STATUS: Formal lithostratigraphic unit.

iii. STRATOTYPE LOCALITY: Cliff sections in Christchurch Bay from west of Sea Road Gap in Barton Cliff to the west, eastwards to Long Mead End (Taddiford Gap) at the eastern extremity of Beacon Cliff.

iv. GRID REFERENCE: SZ 229931 to SZ 262922.

v. LITHOLOGY. Fine sands, largely decalcified, clayey and silty at the base. Glauconite is absent or sparse and fine-grained. Mica is frequent especially towards the top. The sediments are strongly bioturbated and, especially in the lower sand unit, display abundant pellet-lined burrows of *Ophiomorpha*. Rolled flint pebbles occur at the base of a clay unit in the upper part in the east of the basin (Whitecliff Bay). One sharp junction is sometimes recognizable within the formation in the west, between the middle and upper cyclothems, as a slightly indurated ferruginous band (Alum Bay). Division into two wedges occurs through interdigitation with bed J of the Barton Clay Formation. At Barton Cliff the latter is seen to pass laterally westwards into sand of the same facies as bed K. The transition takes place over a distance of about 1 km and the interlocking tongues of sand and clay are complicated by prominent dewatering structures.

vi. BIOTA. This is generally sparse but essentially rather similar to that of the Barton Clay Formation and many of the references given there will suffice here. The biota is, however, more restricted, especially in the upper part which is less marine. No mammals are known.

vii. THICKNESS. 25 m at Barton Cliff; 27·4 m at Alum Bay (according to Curry & Edwards, 1972, but subject to the same tectonic disturbance as the Barton Clay Formation at this locality); and 55 m in Whitecliff Bay (see comment on previously published thickness under definition of Barton Clay Formation, pp. 203–204).

viii. RELATIONSHIPS. Rests with transitional, partially interdigitating, contact on Barton Clay Formation. The top is overlain sharply by the Lower Headon Beds. At the type locality the overlying bed is a thin green sandy clay, uppermost bed K of Burton (1933). This is overlain by a thick shelly lignitic clay (described as bed L of the Barton Beds by Burton (1929) and as the lignite bed of the Lower Headon Beds ('Lower Freshwater Formation') by Wright (1851)). The lignitic clay bed was treated as two different beds by Stinton (1975: 7). Rootlets descend from this horizon into the beds below.

ix. DISTRIBUTION: Limited by the outcrop in the Hampshire Basin. Main sections: Barton and Beacon Cliffs (Burton 1929, 1933), Alum Bay, Whitecliff Bay (Gardner *et al.* 1888), Warwick Slade (Stinton 1970), Totland (Fowler *et al.* 1973). Former sections: Poulner, Fawley (Burton 1933), Brockenhurst (White 1921*b*). Also numerous wells and boreholes (Whitaker 1910, 1917; Freshney 1978).

x. AGE: Late Bartonian (? Marinesian) to early Ludian?; late middle/late Eocene.

xi. SYNONYMY: Equivalent almost exactly to Headon Hill Sand (Prestwich 1846), Barton Sand (Reid 1898) and Upper Bagshot Sand of Tawney (1882). Includes Barton Beds/series in part and comprises Burton's (1929, 1933) beds H (upper) (= Chama Bed s.s.), I and K, except uppermost green clay. Also includes the lower part of the Becton Bunny Beds (Gardner *et al.* 1888) and the Long Mead End Sands (Tawney 1882).

Sands above the 'Hengistbury Beds'. These at Hengistbury may tentatively be included in the Becton Sand Formation as a third, lowest wedge (see Text-fig. 68), but it cannot be confirmed that it was once continuous with known parts of the formation.

Discussion of B.G.S. concept. The current concept of the Barton Formation, as developed by the B.G.S. in the course of mapping the Southampton sheet, is as follows. It comprises Barton Sand, Barton Clay, Huntingbridge division (including Elmore Formation) and sandy clays with *Nummulites variolarius* near the top of the Selsey division (Bracklesham Group). They divide the Barton Formation into a Becton Sand Member (= Barton Sand) and a Barton Clay Member (= the rest) (E. Freshney, personal communication 1981).

Their Barton Formation is, however, mainly a cyclothem and so does not constitute a formation in Hedberg's (1976) sense. Moreover, inclusion of the Selsey division clays causes problems. Sandy clays are interspersed with sandy silts and silty sands in the Selsey division at several levels and localities, not just at the top. Those at the top resemble those lower down in being shelly and having the same clay mineralogy (Curry *et al.* 1968). On the basis of detailed lithology, the latter would have to be included also, and distinctions from the Bracklesham Group would break down. The characteristics of the Barton Clay Formation as a glauconitic or non-glauconitic silty clay with only subsidiary glauconitic clayey sands are important, as are those of the Bracklesham Group as glauconitic sands and sandy clays with intercalated laminated non-glauconitic clays. Curry *et al.* (1968) distinguished three facies in the Fawley Transmission Tunnel and the marked change from the second to the third facies was between the Selsey and Huntingbridge divisions (see Kemp *et al.* 1979). This would thus seem the most appropriate position to place the Bracklesham Group–Barton Clay Formation boundary.

Cyclothems in Christchurch Bay (Text-fig. 2). Two sharp breaks with erosive bases occur in the sequence of the Barton Clay and Becton Sand Formations. They separate three somewhat similar sequences of sediments. The sharp breaks occur at the junctions of Burton's beds A3/B and I/J. The complete idealized sequence of facies is as follows: glauconitic clayey sand/silt (a); glauconitic sandy silty clay (b); glauconitic silty clay (c); non-glauconitic silty clay (d); non-glauconitic sandy silty clay (e); non-glauconitic clayey silty sand (f); and non-glauconitic sand (g). The middle sequence is complete, the lower sequence is almost complete whilst the upper only consists of the last three facies. All three coarsen upwards and therefore in part form similar cyclothems (cycles). The gradual changes within each cycle make the boundaries between Burton's beds (except those coinciding with cycle boundaries) difficult to define, especially when nodule bands or oyster beds are impersistent (e.g. in a restricted section). Certain detailed differences are noticeable between the three cycles. In the lower, the change from one lithology to the next occurs initially by intercalation of a thin bed of the new type. This is followed by further intercalations which become steadily thicker until they exceed and finally exclude those of the old type. In fact in the lower cycle the non-glauconitic sand facies occurs only as intercalations with non-glauconitic silty clay (the non-glauconitic sandy clay facies being cut out); the former never excludes the latter. The middle cycle undergoes only gradual lithological changes, as does the upper. The middle cycle also has a sequence of four nodule bands. The nodules in the first and second bands (B/C and C/D junctions) are subspherical to subovoid; those of the third (E/F junction are subovoid/lenticular; and those of the fourth (within F) are lenticular. Moreover, the Stone Band (G) could be regarded as the final expression of this shape trend, as it is a semi-continuous tabular layer. A slight interruption to the otherwise steady sequence of the middle cycle is the glauconitic sandy interval in the middle of D.

The junction of the Barton Clay and Becton Sand Formations is difficult to recognize. A lithological boundary has previously been taken above the Chama Bed (H) and below the overlying decalcified sands (I). However, when weathered and leached (as at the top of Barton Cliff) the upper part of H appears more sandy and light-coloured and is difficult to distinguish from overlying bed I. To overcome this problem, the formational boundary has been placed at the point where sand first predominates in the sediment. This is roughly in the middle of bed H (base of Chama Bed s.s.) for the lower sand wedge (I) and the top of bed J for the upper sand wedge (K).

The sharp junctions between the lower and middle and between middle and upper cycles have been modified by penecontemporaneous burrowing organisms, so that in places the junctions appear indistinct at close range. These burrows occur throughout the sequence, but are more easily seen at sharp lithological junctions. The burrows often have lined walls (*Ophiomorpha*), which may show glauconite or limonite enrichment. The large burrow systems from the base of B penetrate well into A3, disturbing the sediment, and often contain fossils from B which have thus been introduced secondarily into A3. To further complicate matters, in the lower part of B, some rolled shells occur with patchy black staining which is a preservation diagnostic of A3. It appears that they were derived into B following a phase of erosion which removed the top of A3.

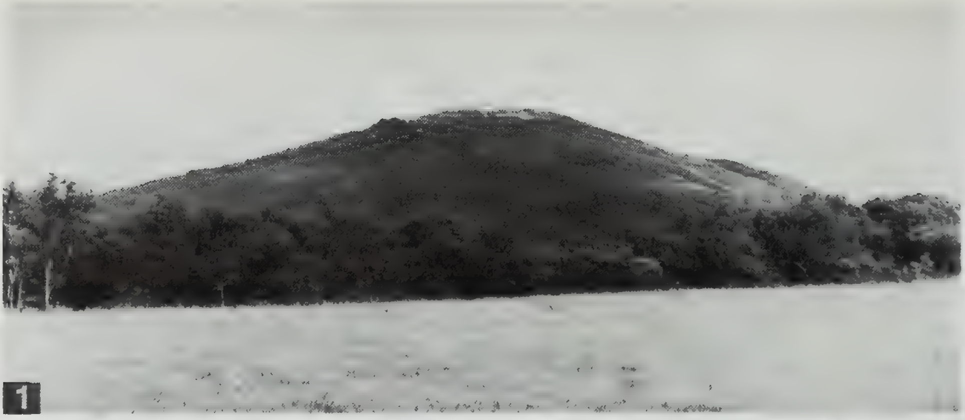
The regressive phase of the upper cycle is continued through the overlying Lower Headon Beds, where the overall facies is non-marine (see Plint (1984) for stratigraphic and sedimentological coverage).

Creechbarrow, Dorset

Of the four localities, this one has yielded by far the largest number of mammalian specimens. On Creechbarrow Hill (SY 921824) over 80 m of clays, sands and conglomerates overlie the 'Dorset Pipe Clay series' and are capped by the Creechbarrow Limestone Formation (Hooker 1977*b*). The mammal fauna is from the latter. The deposits above the pipe clays occur as an outlier and are only known to outcrop on Creechbarrow Hill. There are no natural exposures, so knowledge of the succession is limited to mines in the pipe clays, old pits in the pebbly sands (Hudleston 1902*a*, 1903; Arkell 1947), temporary excavations in the Creechbarrow Limestone and a borehole (Pl. 2; Text-figs 4–6).

Arkell (1947: 233–241) reviewed the history of investigations at the site to that date, but it was not until 30 years later that the limestone was shown to be Bartonian rather than Ypresian ('Lower Bagshot') or Ludian (Bembridge Limestone) in age (Hooker 1977*b*). Hooker (1977*b*) and Preece (1980*a*) also summarized the history of the site.

The succession near the summit. Hudleston's (1902*a*, 1903) descriptions of the succession as exposed in small, now overgrown, pits are detailed, although unfortunately he saw no need to publish a map of these (Hudleston 1902*b*: 169, footnote). The lithic descriptions here are limited to the exposures made between 1975 and 1978 in the region of the limestone for the purpose of collecting its biota (see Text-fig. 5).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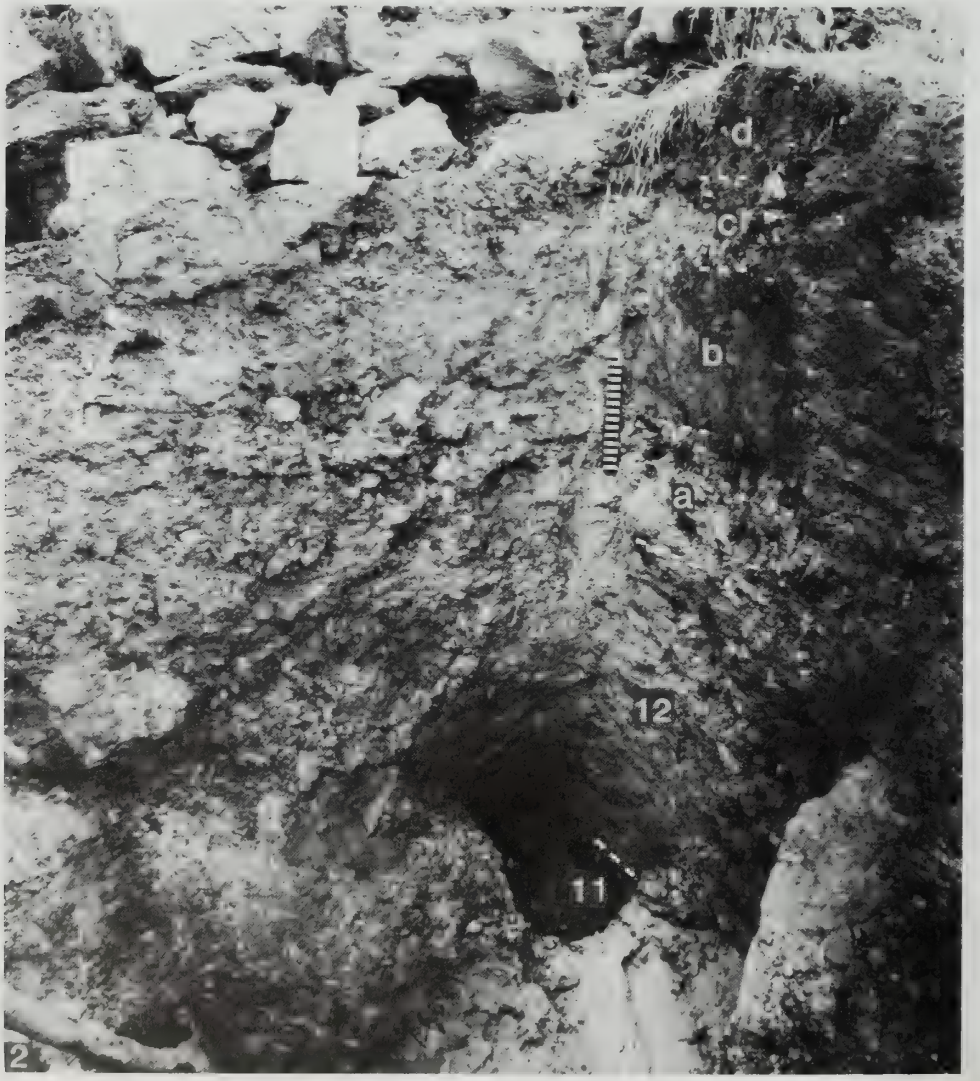

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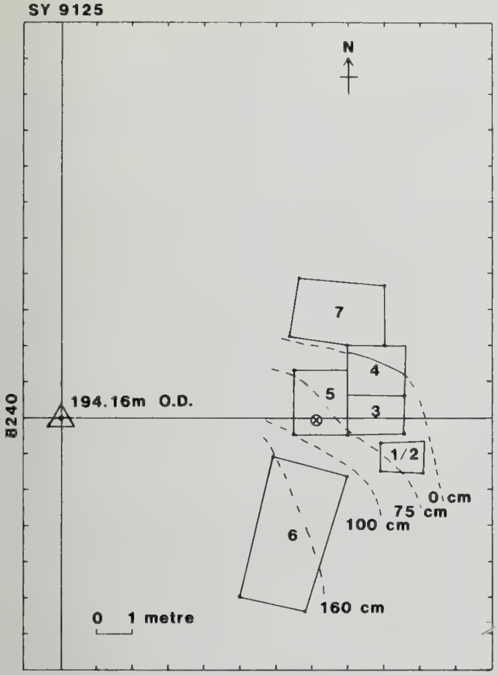
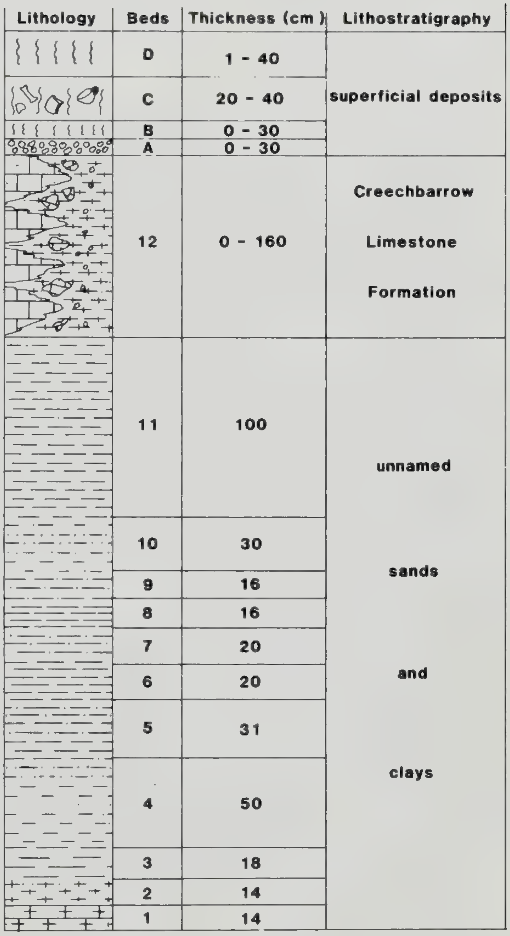

SY 9125
8240
N
194.16m O.D.
7
4
5
3
1/2
6
0 cm
75 cm
100 cm
160 cm
0 1 metre


Lithology
Beds
Thickness (cm)
Lithostratigraphy
D
1 - 40
C
20 - 40
superficial deposits
B
0 - 30
A
0 - 30
12
0 - 160
Creechbarrow Limestone Formation
11
100
10
30
9
16
8
16
7
20
6
20
5
31
4
50
3
18
2
14
1
14
unnamed sands and clays

Text-figure 4 Map of recent Creechbarrow excavations. Spot height of trigonometrical point at summit of the hill is shown. Excavation holes 1 to 7 are numbered. The position of the hand-cored borehole in hole 5 is indicated. Isopachytes of the Creechbarrow Limestone Formation are given.

Text-figure 5 Stratigraphical column of strata exposed in the recent Creechbarrow excavations. For key to lithological symbols of solid deposits, see Text-fig. 2, p. 201. For description of superficial deposits, see p. 211.

The Creechbarrow Limestone Formation. This comprises bed 12 (see Text-fig. 5), a buff marl containing variable sized limestone clasts.

The limestone (sensu stricto): a cream coloured, mottled with buff, soft to hard, massive micritic limestone with drusy sparite, scattered angular to subangular quartz grains up to *c.* 1 mm diameter, oncoliths often containing gastropods (Hudleston's 'horseshoe concretions'), occasional slug plates, moulds of land snails and vertebrate remains. Hard limestone in the recent excavations was mainly encountered in the basal rubbly soil layer (A). None of the

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Plate 2 Creechbarrow, Dorset.

Fig. 1 General view from the south-west. The outcrop of the unnamed sands, clays and gravels is marked by the dark cover of bracken (*Pteridium aquilinum* (L.)). The outcrop of the Creechbarrow Limestone Formation at the summit is marked by the light cover of grass.

Fig. 2 Section in north-east corner of Hole 6. For explanation of bed numbers see Text-fig. 5 (above) and text. Scale is in centimetre units.

limestone appeared to be truly *in situ*, although Hudleston (1902*a*: fig. 2) claimed to have found it so in his 'summit pit'.

The buff marl: a buff calcareous silty clay with abundant angular to subangular quartz grains up to 1 mm diameter and containing limestone clasts (see above). It also contains oncoliths often containing gastropods, snail opercula, slug plates, vertebrate remains and derived silicified Cretaceous bryozoans.

Interpretation of bed 12. The size and abundance of limestone clasts within the buff marl increases towards the centre of the summit of the hill, until it finally consists of a mass of large limestone boulders with the marl simply filling the narrow gaps in between. This suggests that the marl may be the result of decomposition *in situ* of softer parts of the limestone.

A piece of soft limestone was broken down in dilute acetic acid and yielded a very poorly sorted sand with minor silt and clay components and vertebrate debris. The greater proportion of clay which occurs in the marl suggests that the above interpretation of the origin of the marl is too simple. It is perhaps more likely that there was originally a series of passage beds from manganiferous clay (bed 11) through marl to the limestone, which has become greatly modified by solution. Today, the marl and limestone lithologies do not form discrete beds. Sequences of marl through to limestone occur in several parts of the 'Fluvio-marine series' in the Isle of Wight (see Insole 1972) and some may be comparable. That solution must almost certainly have occurred is indicated by the abundance in the marl of oncolith-enclosed gastropods, *Bembridgia* opercula, slug plates and vertebrate remains, especially mammals, all of which have been encountered more sparsely in the soft limestone.

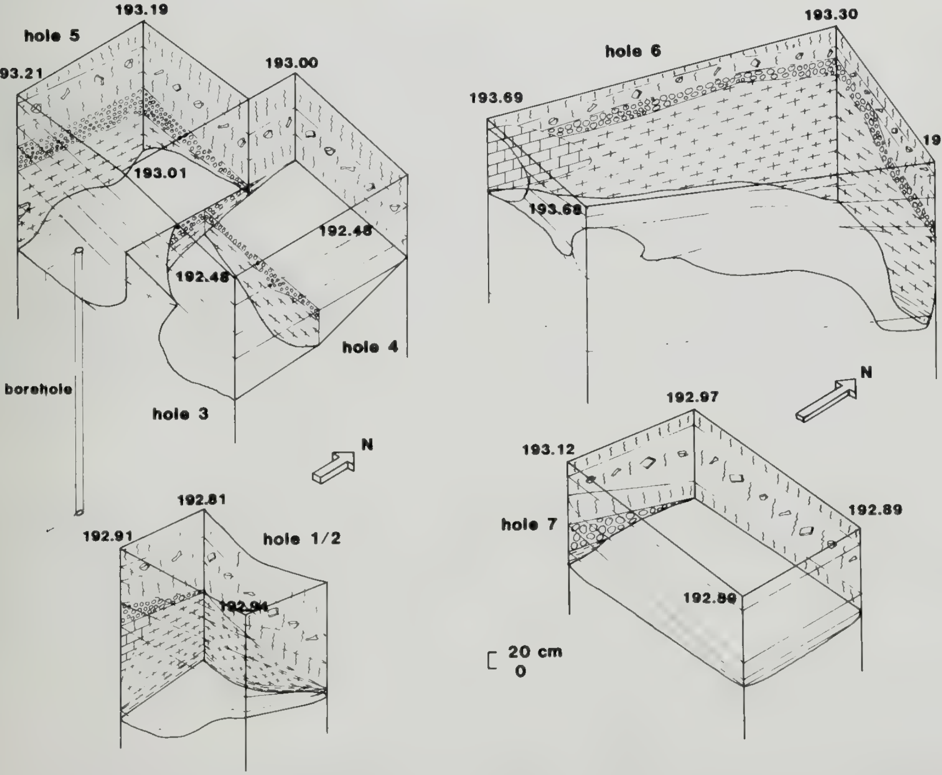
Keeping (1912: 131) noted that 'there is everywhere evidence of great disturbance of the strata, whether we refer this chiefly to large movements of faulting and overthrust, or the more superficial action of landslips, soil creep etc. The result has been a kneading up together of various deposits, so as to produce in many parts a mass much resembling some boulder clays'. In the recent excavations this statement is supported not only by the jumbled nature of the various limestone blocks embedded in the buff marl but also by a detached lobe of the manganiferous clay enclosed within the buff marl in the SW corner of Hole 5. Evidence for bedding is notably lacking. It is quite likely that the disturbance and solution features could have resulted from permafrost and solifluction activity during the Pleistocene.

Beds 1–11. These all consist of manganiferous, very poorly sorted clay/silt/sand in which the grains are subangular to subrounded and up to 1 mm in diameter (see Text-fig. 5).

Bed 11: pale brown sandy silty clay with occasional angular fragments of flint. This formed the floor of the excavations, in which it was exposed in places. It also occurred in the top metre of the shallow hand-cored borehole put down from the floor of Hole 5. Beds 1–10 were exposed only in this shallow borehole.
Bed 10: pale brown clayey silty sand.
Bed 9: pale brown very sandy silty clay.
Bed 8: pale grey silty clay with low sand content.
Bed 7: pale brown very sandy silty clay.
Bed 6: pale grey very silty clay with low sand content.
Bed 5: pale grey sandy silty clay.
Bed 4: pale brown slightly clayey silty sand, the clay content reducing considerably in middle of bed.
Bed 3: pale brown very clayey silty sand.
Bed 2: very pale grey calcareous silty sand.
Bed 1: whitish buff very calcareous silty sand with small ovoid and tubular calcareous concretionary bodies (? oncoliths) 2–5 mm in diameter.

The base of the hand-cored borehole was at 187·8 m OD. After an unrecorded interval of 3·9 m, at 183·9 m OD is the top of an English China Clays (E.C.C.) borehole which was put down in 1973 at SY 92138 82367 and penetrated 72·2 m of sediment, the base being at 111·7 m OD. The recovery was very incomplete but the lithology was recorded as mainly hard sand or loamy sand, with frequent layers of flints which finally caused the drilling rods to jam and twist off before the pipe clays were reached. At about 150 ft down (138 m OD) a different lithology was recorded, described as 'almost white silty clay w. brown yellow mottle and veining throughout'. This might represent the brick clay, exposed in Mr Bond's brickyard; but this stratum was recorded by Arkell (1947) as occurring from 20–80 ft below the limestone. There are many inconsistencies and gaps in our knowledge concerning the strata below the limestone and detailed logging of these would be a worthwhile future project. I am very grateful to English China Clays for allowing me to consult and reproduce data from their borehole log of Creechbarrow.

The Superficial Deposits. Bed A is very variable in thickness and probably resulted from weathering of the limestone, perhaps once naturally exposed at the surface. Hudleston (1902*a*: 250) surmised that a limestone needle was once exposed at the summit of the hill and later artificially levelled to produce limestone rubble (= bed A herein). If so, then the fine sandy soil of bed B was the natural soil formed subsequent to the building of a 'lodge' of which only the foundations now remain. This homogeneous horizon is devoid of human debris and wedges out rapidly westwards and summitwards in Hole 6. Hudleston (1902*a*: 253) later contradicted his own surmise when he suggested rapid disintegration of the limestone 'when exposed to the atmosphere' as the only explanation for absence of fragments on the flanks of the hill and its lack of use as a building stone. It seems more likely, therefore, that bed B was the natural soil formed before human occupation. Bed C was found to contain fragments of limestone, pottery, glass and roofing 'slate' (composed of Purbeck limestone) and a human phalangeal bone, as well as numerous black (? burnt) patches. This could have formed during occupation and/demolition of the 'lodge'. Bed D, the modern topsoil, has presumably developed since demolition, which, according to Hudleston (1902*b*), took place in the mid 18th Century.



Text-figure 6 Three-dimensional diagrams of stratigraphy in Creechbarrow holes 1–7. For lithological explanation see Text-figs 2, 5 and text. Figures are spot heights O.D. in metres of corners of holes measured from trigonometrical point. The floors of the excavations are shown blank.

Fragments of soft red limestone, perhaps representing Keeping's (1910: 437) 'Cherry Marl' (a workmen's term, given informal bed status by Cooper, 1976: 9), were found in bed C. Evidence of probable burning in bed C, the omission of any mention of the bed in Keeping's (1912: 130–131) or Hudleston's (1902*a*, *b*, 1903) detailed sections and its absence *in situ* in the sections exposed during the recent excavations all suggest that this rock has been discoloured by fire: a test, which involved burning a soft piece of Creechbarrow Limestone, produced a comparable red colour.

Structure. Hudleston (1902*a*: 249) calculated a dip of 10°–12° N for the Creechbarrow Limestone. Bloomfield (1913) showed similar dips for the underlying beds, but in this case apparently on the eastern side dipping westwards. Hudleston showed the limestone to continue some way down the northern slope of the hill and Arkell's (1947: 233) map reflects this. In the recent excavations, the base of the limestone appeared to rise at the northern end, the outcrop edge swinging sharply to the west, thus suggesting an east–west striking synclinal structure for the beds at the summit (Text-figs 4, 6). No excavations were made on the northern slope during the recent visits, only flint gravel being seen there in a long shallow trench which may be the remains of one of Hudleston's pits. It cannot be confirmed that limestone on the north face is *in situ*; but equally it cannot be affirmed that the dip of the beds in the recent excavations could not be due to recent earth movements (e.g. soil creep, solifluction, slumping due to mining of the pipe clay, etc.). Palaeogene sedimentology and structure of the whole area of the western Hampshire Basin (Wareham Basin) is the subject of a recent study by Plint (1981, unpublished Ph.D. thesis, Oxford), some aspects of which have been published (Plint 1982, 1983).

Systematic palaeontology

The taxa described are listed below with locality data (Table 1). The taxonomic order is essentially founded on Simpson (1945) but incorporating various subsequent modifications. Some of these are discussed under the relevant groups. Others concern the placing of Cetacea after Condylarthra from which they are considered to be derived (e.g. see Gingerich & Russell 1981); and the basic twofold division of Eutheria into 'insectivore-primate-rodent' and 'carnivore-ungulate' groups as advocated by Lillegraven (1969).

Dental nomenclature diagrams for various key groups explain the terms used in this work (Text-figs 8, 31, 43 and 54).

For mammalian ranges after the Bartonian, Ludian is used in preference to Priabonian and Stampian in preference to Rupelian, because of difficulties of correlation within each pair, in contrast to the relative ease of referring relevant European mammal faunas to the Ludian and Stampian. See Cavelier (1979) for information on correlating Ludian and Stampian with Priabonian and Rupelian.

See also the notes on taxonomic procedure, p. 195.

Table 1 The English Bartonian mammals and their localities: E – Elmore, H – Hengistbury, C – Creechbarrow, B – Barton, beds C–F. All are Class MAMMALIA Linnaeus, Subclass THERIA Parker & Haswell.

	Page	E	H	C	B
Infraclass METATHERIA Huxley	215				
Superorder MARSUPIALIA Illiger, Order MARSUPICARNIVORA Ride	215				
Superfamily DIDELPHOIDEA Gray	215				
Family DIDELPHIDAE Gray	215				
Subfamily DIDELPHINAE Gray, Tribe DIDELPHINI Gray	215				
Genus *Amphiperatherium* Filhol	216				
1. *Amphiperatherium* aff. *goethei* Crochet	216	–	–	×	–
2. *Amphiperatherium fontense* Crochet	220	–	–	×	–

Table 1 (*continued*)

	Page	E	H	C	B
Infraclass EUTHERIA Gill	222				
Order PROTEUTHERIA Romer	222				
Family PANTOLESTIDAE Cope	222				
3. ? Pantolestidae, gen. et sp. indet.	222	–	–	×	–
Order LIPOTYPHLA Haeckel	223				
Suborder ERINACEOMORPHA Saban	223				
Family AMPHILEMURIDAE Heller	223				
Genus *Gesneropithex* Hürzeler	224				
4. *Gesneropithex figularis* sp. nov.	234	–	–	×	–
Family NYCTITHERIIDAE Simpson	239				
Subfamily NYCTITHERIINAE Simpson	239				
Genus *Scraeva* Cray	240				
5. *Scraeva* sp. indet.	241	–	–	×	–
Order CHIROPTERA Blumenbach	241				
Suborder MICROCHIROPTERA Dobson	241				
Family indet.	241				
6. gen. et sp. indet. 1	241	–		×	×
7. gen. et sp. indet. 2	243	–	–	×	–
8. gen. et sp. indet. 3	245	–	–	×	–
9. gen. et sp. indet. 4	245	–	–	×	–
Order PRIMATES Linnaeus	245				
Suborder PROSIMII Illiger	245				
Infraorder TARSIIFORMES Gregory	245				
Family OMOMYIDAE Trouessart	245				
Subfamily MICROCHOERINAE Lydekker	245				
Genus *Nannopithex* Stehlin	249				
10. *Nannopithex quaylei* sp. nov.	249	–	–	×	–
11. *Nannopithex* sp. 1	251	-		×	–
Genus *Pseudoloris* Stehlin	252				
12. *Pseudoloris* cf. *crusafonti* Louis & Sudre	256	–	–	×	–
Genus *Microchoerus* Wood	257				
13. *Microchoerus wardi* sp. nov.	259	–	–	×	–
14. *Microchoerus creechbarrowensis* sp. nov.	261	–	–	×	–
Infraorder LEMURIFORMES Gregory	267				
Family ADAPIDAE Trouessart	267				
Subfamily ADAPINAE Trouessart	267				
Genus *Europolemur* Weigelt	267				
15. *Europolemur collinsonae* sp. nov.	270	–	–	×	–
Genus *Leptadapis* Gervais	274				
16. *Leptadapis* aff. *magnus* (Filhol)	278	–	–	×	–
17. Adapinae, gen. et sp. indet.	282		–	×	–
Order RODENTIA Bowdich	282				
Suborder SCIUROGNATHI Tullberg	282				
Infraorder PROTROGOMORPHA Zittel	282				
Family PARAMYIDAE Miller & Gidley	282				
Subfamily MANITSHINAE Simpson	283				
Genus *Plesiarctomys* Bravard	283				
18. *Plesiarctomys curranti* sp. nov.	283	–	–	×	–
19. *Plesiarctomys hurzeleri* Wood	288	–	–	×	–
20. ? Manitshinae, gen. et sp. indet.	290	–	–	×	–
Subfamily AILURAVINAE Michaux	291				
Genus *Ailuravus* Rütimeyer	291				
21. *Ailuravus stehlinschaubi* Wood	293	–	–	×	–

Table 1 (*continued*)

Table 1 *(continued)*

		Page	E	H	C	B
	Infraorder uncertain, Superfamily THERIDOMYOIDEA Alston	295				
	Family PSEUDOSCIURIDAE Zittel	298				
	Genus *Sciuroides* Major	300				
22.	*Sciuroides rissonei* sp. nov.	301	–	–	×	–
	Genus *Treposciurus* Schmidt-Kittler	307				
	Treposciurus helveticus Schmidt-Kittler	308				
	Treposciurus helveticus helveticus Schmidt-Kittler	308				
23.	*Treposciurus helveticus preecei* subsp. nov.	309	–	–	×	–
	Genus *Suevosciurus* Dehm	315				
24.	*Suevosciurus authodon* sp. nov.	315	–	–	×	–
	Order APATOTHERIA Scott & Jepsen	327				
	Family APATEMYIDAE Matthew	327				
	Genus *Heterohyus* Gervais	329				
25.	*Heterohyus* cf. *sudrei* Sigé	330	–	–	×	–
26.	*Heterohyus* aff. *nanus* Teilhard	330	–	–	×	–
27.	*Heterohyus morinionensis* sp. nov.	331	–	–	×	–
	Heterohyus spp. indet.	334	–	–	×	–
	Order CARNIVORA Bowdich	336				
	Superfamily MIACOIDEA Cope	336				
	Family MIACIDAE Cope	336				
	Subfamily MIACINAE Cope	336				
	Genus *Miacis* Cope	336				
28.	? *Miacis* sp. indet.	336	–	–	×	–
29.	? Miacinae, gen. et sp. indet.	338	–	–	×	–
	Order CONDYLARTHRA Cope	338				
	Family PAROXYCLAENIDAE Weitzel	338				
	Genus *Vulpavoides* Matthes	339				
30.	*Vulpavoides cooperi* sp. nov.	340	–	–	×	–
	Order CETAÇEA Brisson	342				
	Suborder ARCHAEOCETI Flower	342				
	Family DORUDONTIDAE Miller	342				
	Genus *Zygorhiza* True	342				
31.	*Zygorhiza wanklyni* (Seeley)	342	–	–	–	×
	Family BASILOSAURIDAE Cope	342				
	Genus *Basilosaurus* Harlan	342				
32.	*Basilosaurus* sp. indet.	342	–	–	–	×
	Order PERISSODACTYLA Owen	342				
	Superfamily EQUOIDEA Hay	342				
	Family PALAEOTHERIIDAE Bonaparte	342				
	Genus *Propalaeotherium* Gervais	343				
33.	*Propalaeotherium* aff. *parvulum* (Laurillard)	343	×	–	×	–
	Genus *Lophiotherium* Gervais	347				
34.	*Lophiotherium siderolithicum* (Pictet)	347	–	–	×	–
	Genus *Plagiolophus* Pomel	353				
	Plagiolophus curtisi sp. nov.	353				
35.	*Plagiolophus curtisi curtisi* subsp. nov.	356	–	–	–	×
36.	*Plagiolophus curtisi creechensis* subsp. nov.	364	–	–	×	–
	Genus *Palaeotherium* Cuvier	371				
37.	*Palaeotherium* aff. ?*muehlbergi* Stehlin	371	–	–	–	×
38.	*Palaeotherium* sp. indet.	373	×	–	–	–
	Suborder ANCYLOPODA Cope	374				
	Family LOPHIODONTIDAE Gill	374				
	Genus *Lophiodon* Cuvier	374				
39.	*Lophiodon* cf. *cuvieri* Filhol	374	×	–	–	–
40.	*Lophiodon* cf. *lautricense* Noulet	376	–	×	–	–

Table 1 *(continued)*

	Page	E	H	C	B
Order ARTIODACTYLA Owen	376				
Suborder PALAEODONTA Matthew	376				
Superfamily DICHOBUNOIDEA Gill	376				
Family DICHOBUNIDAE Gill	376				
Genus *Hyperdichobune* Stehlin	376				
41. *Hyperdichobune* sp. 1	376	–	–	×	–
42. ? *Hyperdichobune* sp. 2	379	–	–	×	–
Family MIXTOTHERIIDAE Pearson	381				
Genus *Mixtotherium* Filhol	381				
43. *Mixtotherium* aff. *gresslyi* Rütimeyer	383	–	–	×	–
44. ? *Mixtotherium* sp. indet.	389	–	–	×	–
Family CEBOCHOERIDAE Lydekker	389				
Genus *Cebochoerus* Gervais	390				
45. *Cebochoerus minor* Gervais	391	–	–	–	×
46. *Cebochoerusrobiacensis*Depéret	398	–	–	×	–
Genus *Acotherulum* Gervais	399				
47. *Acotherulum campichii* (Pictet)	400	–	–	×	–
Suborder ANCODONTA Matthew	404				
Superfamily ANTHRACOTHERIOIDEA Gill	404				
Family HAPLOBUNODONTIDAE Pilgrim	404				
Genus *Haplobunodon* Depéret	404				
48. *Haplobunodon venatorum* sp. nov.	404	–	–	×	–
Family ? CHOEROPOTAMIDAE Owen	409				
Genus ? *Choeropotamus* Cuvier	409				
49. ? *Choeropotamus* sp. indet.	409	–	–	×	–
Superfamily ANOPLOTHERIOIDEA Bonaparte	409				
Family ANOPLOTHERIIDAE Bonaparte	409				
Subfamily DACRYTHERIINAE Depéret	409				
Genus *Dacrytherium* Filhol	410				
50. *Dacrytherium elegans* (Filhol)	410	–	–	×	–
Suborder TYLOPODA Illiger	412				
Superfamily XIPHODONTOIDEA Flower	412				
Family XIPHODONTIDAE Flower	412				
Genus *Dichodon* Owen	412				
51. *Dichodon* cf. *cervinus* (Owen)	413	–	–	×	–
52. *Dichodon* sp. indet.	414	–	–	×	–
53. Artiodactyla, fam., gen. et sp. indet.	414	–	–	×	–

Class **MAMMALIA** Linnaeus 1758
Subclass **THERIA** Parker & Haswell 1897
Infraclass **METATHERIA** Huxley 1880
Superorder **MARSUPIALIA** Illiger 1811
Order **MARSUPICARNIVORA** Ride 1964
Superfamily **DIDELPHOIDEA** Gray 1827
(rank emend. Osborn 1910)

Family **DIDELPHIDAE** Gray 1827
Subfamily **DIDELPHINAE** Gray 1827
(rank emend. Simpson 1927)

Tribe **DIDELPHINI** Gray 1827
(rank emend. Crochet 1979)

Type genus. *Didelphis* L. 1758. Recent, North and South America.

Included genera. See Crochet (1979: 368) for long list of genera. The only two in the European Tertiary are *Peratherium* Aymard 1850 and *Amphiperatherium* Filhol 1879.

Range. Late Palaeocene to Eocene, Miocene to Recent, South America; early Eocene to early Miocene, Pleistocene to Recent, North America; and early Eocene to middle Miocene, Europe (from Crochet 1979).

Diagnosis. See Crochet (1979: 368).

Dental nomenclature and formula. Dental nomenclature essentially follows the eutherian pattern (see Text-fig. 8, p. 222) with the exception of the five upper molar stylar cusps. These are lettered A to E (mesially to distally) and occupy the following positions of the eutherian stylar cusps: A (parastyle), B (stylocone), C (mesostyle), E (metastyle); D is between C and E (see Crochet 1980: fig. 2). Homologies are disputed (Clemens 1979: 200–201, fig. 11.1). Length and width measurements follow Clemens (1966: 4, text-fig. 1), with the addition of the length of the protocone lobe.

Crochet (1979, 1980) referred frequently to the length of the protofossa as an important character. This term equals the trigon basin (see Van Valen 1966: text-fig. 1; Szalay 1969: text-fig. 1), and is difficult to measure when worn. A more appropriate structure to describe the same character is the protocone lobe. This is the lingual section of the upper molar delimited buccally by the postflexus and may be what Crochet actually meant.

Numbering and naming of the cheek teeth is also disputed (see Clemens 1979: 202–203; Crochet 1980: 25–26). A conservative approach is adopted here, the four molariform teeth being referred to as $M\frac{1}{1}-\frac{4}{4}$.

Genus *AMPHIPERATHERIUM* Filhol 1879

(See Crochet 1980 for synonymy list)

Type species. *A. frequens* (Meyer 1846) Crochet 1977. Oligocene; Weissenau, West Germany.

Included species. *A. brabantense* Crochet 1979; *A. giselense* (Heller 1936) Crochet 1977; *A. bourdellense* Crochet 1979; *A. minutum* (Aymard 1846) Crochet 1977; *A. goethei* Crochet 1979; *A. lamandini* (Filhol 1876*b*) Crochet 1979; *A. maximum* Crochet 1979; *A. bastburgense* Crochet 1979; *A. fontense* Crochet 1979; *A. ambiguum* (Filhol 1877*b*) Crochet 1979; and *A. exile* (Gervais 1852) Crochet 1979.

Range. Early Eocene to middle Miocene, Europe.

Diagnosis. See Crochet (1980: 59).

Amphiperatherium aff. ***goethei*** Crochet 1979

(Pl. 3, figs 1–6; Text-fig. 7A; Table 2)

v. *1977b* *Peratherium* sp. 1; Hooker: 141.
v. *1980* *Amphiperatherium* sp. 1; Hooker & Insole: 37.

Holotype of species. Left M^3 (UM Bux68.89). Middle Lutetian; Bouxwiller, Bas-Rhin, France.

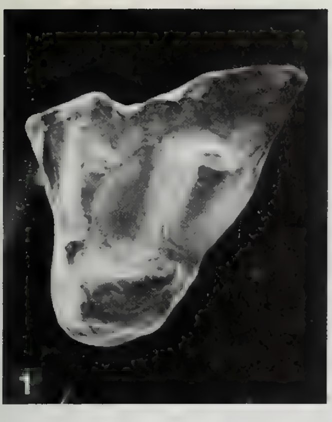
Range of species. Sparnacian to Lutetian, France.

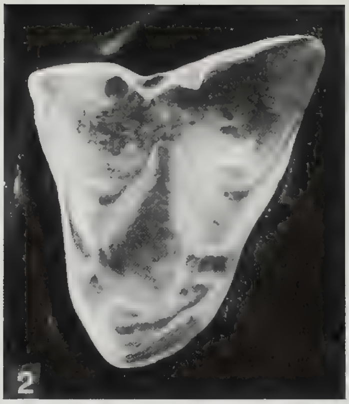
Diagnosis of species. See Crochet (1979: 371)

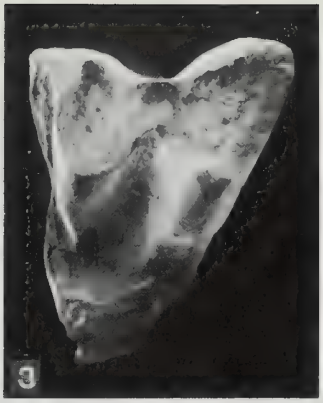
Material. Right M^1 (M37110); left M^2 (M35631); right M^2 (M35632); left M^3 (M35633); two right M^3 protocone lobe fragments (M35634–5); right P_2 (M35636); left M_2 (M37112); left M_3 (M35637); left M_4 (M35638); left and right $M_{1/2/3}$ talonid fragments (M35642–3); right M_3 trigonid fragment (M35640); left M_4 trigonid fragment (M37113); two right M_4 trigonid fragments (M35641, M37114).

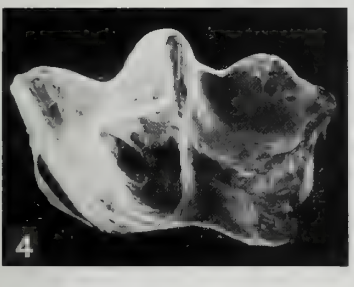
Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

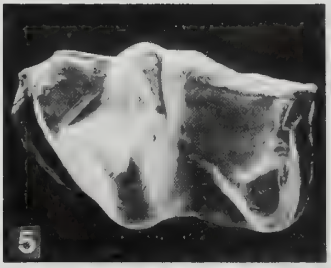
Description. M^1: The tooth has an oblique appearance caused by the mesially positioned protocone and acute distobuccal angle. Cusps B and D are subequal, C is slightly smaller and slightly nearer to D than to B. B is nearer to A than to C. The ectoflexus is moderately shallow and asymmetrical. The paracingulum narrows in front of the paracone. The protocone lobe is

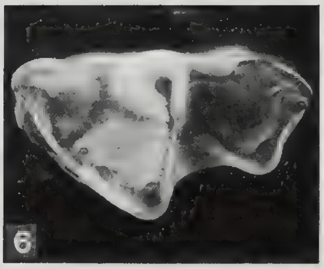


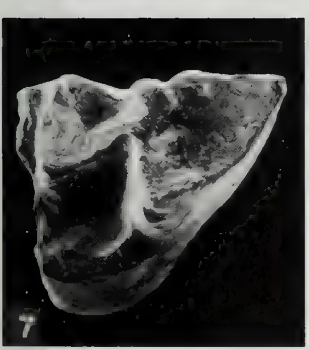


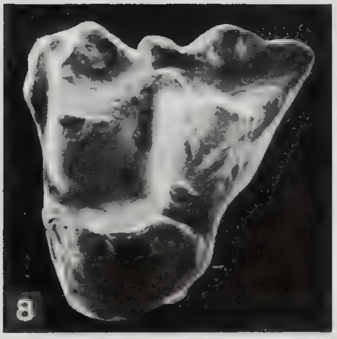


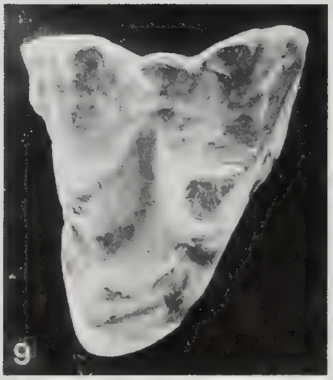


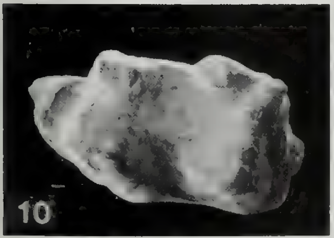


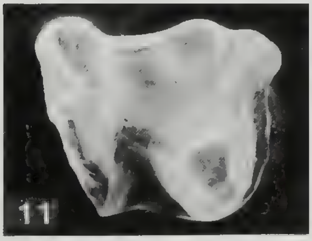












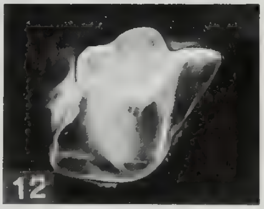


Plate 3 Scanning electron micrographs of occlusal views of molars of *Amphiperatherium* from Creechbarrow.

Figs 1–6 *Amphiperatherium* aff. *goethei* Crochet, ×24. Fig. 1, right M^1 (reversed) (M37110). Fig. 2, right M^2 (reversed) (M35632). Fig. 3, left M^3 (M35633). Fig. 4, left M_2 (M37112). Fig. 5, left M_3 (M35637). Fig. 6, left M_4 (M35638). See p. 216.

Figs 7–12 *Amphiperatherium fontense* Crochet, ×16. Fig. 7, left M^1 (M35390). Fig. 8, left M^2 (M35602). Fig. 9, right M^3 (reversed) (M37093). Fig. 10, left M_1 (M35612). Fig. 11, left $M_{2/3}$ with broken trigonid (M35391). Fig. 12, right M_4 talonid fragment (reversed) (M35617). See p. 220.

slightly abraded lingually and distally and it is not known whether it was rounded or angular lingually.

M^2: Cusps B and D are subequal, B being only very slightly larger. C is slightly smaller and significantly closer to D than to B. On M35632, B is equidistant between A and C, but on M35631 nearer to A and separated from C by a deep fissure. The ectoflexus is moderately shallow and asymmetrical. On M35632, the paracingulum narrows as on M^1 but insignificantly on M35631. The protocone lobe is angular lingually.

M^3: Cusps C and D are subequal and smaller than B. C is equidistant between B and D, and B is closer to A than to C. The ectoflexus is fairly deep and symmetrical. The paracingulum almost disappears in front of the paracone. The protocone is angular lingually.

On the three upper molar types represented, dilambdodonty is marked, narrowing the stylar shelf near cusp C so that it is less than half the width that it is at the metacone. The teeth are relatively short, probably in part due to the shortness of the metastylar wing. The protocone lobe is long relative to tooth length. The paraconule and metaconule are prominent, especially the latter; and so are the pre- and post-paraconule and premetaconule cristae.

M_2: The outline is relatively elongate (length about twice the width); and the lengths of trigonid and talonid are approximately equal. The protoconid is slightly mesial to the metaconid. The paraconid is about $\frac{3}{4}$ the height of the metaconid and their bases are of equal length. The entoconid is low and elongate oval in occlusal view. The postcristid is broken between the entoconid and hypoconulid. The hypoconulid is chipped and it is difficult to estimate its distal saliency. The slightly buccally concave cristid obliqua joins the protoconid midway between the buccal edge and the trigonid notch. The postmetacristid is restricted basally. The precingulid terminates at the protoconid.

M_3: Outline and trigonid/talonid proportions are as on M_2. The protoconid is exactly opposite the metaconid. The paraconid is about $\frac{3}{4}$ the height of the metaconid. The entoconid and hypoconulid are broken away. The cristid obliqua is more strongly concave buccally than in M_2 and joins the protoconid midway between the buccal and lingual tooth margins. The postmetacristid is restricted basally. The precingulid extends slightly round the protoconid and the ectocingulid bears a worn ectostylid.

M_4: The talonid is $\frac{3}{4}$ the width of the trigonid. The protoconid is exactly opposite the metaconid. The paraconid is $\frac{3}{4}$ the height of the metaconid and nearly twice as long basally; and the valley between is open. The entoconid and hypoconulid are chipped but the latter is closer to the former than to the hypoconid. The cristid obliqua has the same orientation and protoconid attachment position as on M_3. There is no postmetacristid. The precingulid terminates at the protoconid.

Measurements are given in Table 2.

Table 2 Tooth length (l) and width (w) and length of upper molar protocone lobe (lp) of *Amphiperatherium* aff. *goethei* and *A. fontense* from Creechbarrow. Measurements in millimetres.

Amphiperatherium aff. *goethei*

No.	Tooth	l	w	lp
M37110	M^1	1·63	1·70	0·90
M35631	M^2	1·75	2·02	1·00
M35632	M^2	1·72	1·88	1·05
M35633	M^3	1·53	1·93	0·90
M37112	M_2	1·88	1·17	–
M35637	M_3	(1·77)	1·18	–
M35640	M_3	–	1·17	–
M35638	M_4	1·77	1·15	–
M37113	M_4	–	0·97	–
M35641	M_4	–	1·00	–
M37114	M_4	–	1·00	–

Amphiperatherium fontense

No.	Tooth	l	w	lp
M35390	M^1	2·30	2·60	1·40
M37090	M^1	2·35	2·45	1·20
M37091	M^1	(2·50)	2·30	1·25
M35601	M^2	(2·60)	(2·65)	1·55
M35602	M^2	2·50	2·70	1·55
M35603	M^2	–	–	1·55
M35600	M^2	–	(2·30)	1·40+
M35604	M^2	2·55	2·75	1·45
M37092	M^2	(2·65)	(2·65)	1·60
M37093	M^3	2·50	2·80	1·35
M35612	M_1	2·35	1·30	–
M35396	M_1	–	1·15	–

Affinities. Few specimens of different tooth types are available for one to judge intraspecific variation. However, the common occurrence of certain characters on different teeth, together with narrow size limits, points to the presence of an homogeneous assemblage. Both in size and morphology, this assemblage is closest to *A. goethei*, which is also defined on a relatively small sample. The principal differences from this species are as follows:

Upper molars with: 1. cusp C not doubled;
2. slightly greater dilambdodonty;
3. longer protocone lobe;
4. stronger postparaconule and premetaconule cristae;
5. slightly deeper M^1 ectoflexus.
Lower molars with: 6. slightly narrower outline;
7. slightly higher paraconid;
8. slightly buccally concave cristid obliqua.
Overall size: 9. slightly smaller (see Text-fig. 7A).

These differences, however, should not be overemphasized. A doubled cusp C is not constant in *A. goethei*; characters 2, 4 and 8 are very slight in degree; and 5 could well be within the range of intraspecific variation.

The stylar shelf in *A. goethei* was stated by Crochet (1979: 371, 1980: 89) to be normally developed, but, according to his figures, it differs little from that of *A. giselense*, which is stated (1980: 63) to be of reduced width. In *A.* aff. *goethei*, because of the slightly greater dilambdodonty, the stylar shelf adjacent to cusp C is even more reduced.

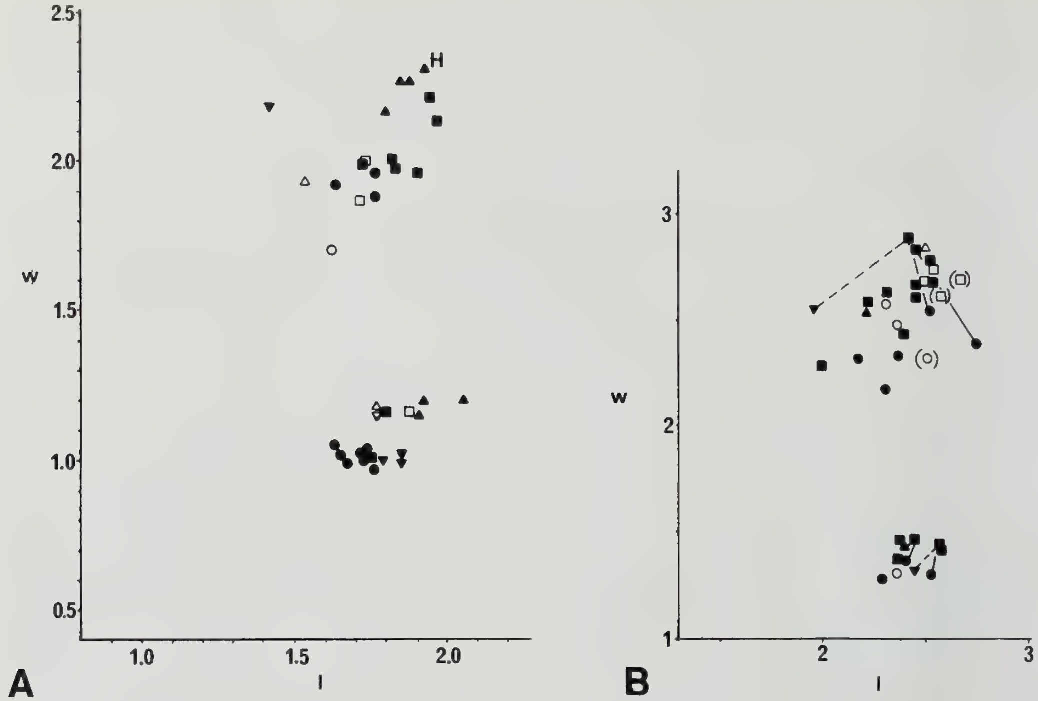
A. aff. *goethei* can be distinguished from the rather similar and highly variable but slightly smaller *A. minutum* by:

Upper molars with: 1. stronger cusp C;
2. slightly greater dilambdodonty than even the most extreme variations of *A. minutum*;
3. relatively shorter outline;
4. relatively much longer protocone lobe;
5. more prominent paraconule and metaconule and their cristae.
Lower molars with: 6. more mesial protoconid;
7. lower entoconid;
8. more lingual protoconid attachment of cristid obliqua;
9. cristid obliqua slightly concave buccally;
10. longer M$_{1-3}$ talonids.

Crochet (1980: 79–88) documented a stratigraphical morphocline within *A. minutum*, ranging from late Bartonian to middle Oligocene. The earlier forms show the most differences from *A.* aff. *goethei* in character 2 and size. The later forms show the most differences from *A.* aff. *goethei* in characters 1 and 3.

The Creechbarrow assemblage shows no special similarity (except size) with the smaller of the two unnamed species of *Amphiperatherium* described from the Lower Headon Beds of Hordle Cliff by Cray (1973) as '*Peratherium* sp. A'. The latter has upper molars with much shallower ectoflexus, larger cusp C, slightly less dilambdodonty, broader paracingulum; and lower molars with relatively broader outline, shorter talonid, straight cristid obliqua, larger obliquely elongate entocristid, frequent postcristid between entoconid and hypoconulid and broader talonid on M$_4$.

Crochet (1980) considered *A. goethei* and *A. lamandini* to be closely related and to have an ancestor–descendant relationship. The youngest record of *A. goethei* is from the middle to late Lutetian, the oldest of *A. lamandini* late Ludian (with a doubtful record from the Marinesian of Grisolles). The Creechbarrow assemblage is stratigraphically intermediate between *A. goethei* and *A. lamandini*. In its differences 1, 3 and 7 from *A. goethei*, *A.* aff. *goethei* shows trends



Text-figure 7 Scatter diagrams of length (l) against width (w) of upper and lower molars of *Amphiperatherium*. In both diagrams the upper group of plots are upper, the lower group lower molars. ○ = M$\frac{1}{1}$; □ = M$\frac{2}{2}$; △ = M$\frac{3}{3}$; ▽ = M$\frac{4}{4}$. H = Holotype. Measurements in millimetres.

A. Solid symbols = *A. goethei* from Bouxwiller (H indicates holotype); hollow symbols = *A.* aff. *goethei* from Creechbarrow. Bouxwiller data are from Crochet (1980: fig. 104).

B. *A. fontense* from Fons 4 and La Bouffie (solid symbols) and Creechbarrow (hollow symbols). Associated teeth joined by solid and dotted lines belong to holotype from Fons 4. Fons 4 and La Bouffie data are from Crochet (1980: fig. 133).

towards *A. lamandini*, but not in the other characters. It is, however, difficult to evaluate all of these in terms of constancy, although at least some such characters as 6 and 8 appear to give more individuality to the Creechbarrow assemblage, in a direction different from that of *A. lamandini*. It may eventually be found that the Creechbarrow assemblage represents a new, possibly endemic, species, but it is here nomenclaturally linked with its closest relative.

Amphiperatherium fontense Crochet 1979
(Pl. 3, figs 7–12; Text-fig. 7B; Table 2)

v. *1977b* *Peratherium* sp. 2; Hooker: 141.
v. *1980* *Amphiperatherium* sp. 2; Hooker & Insole: 37.

HOLOTYPE. Palate and mandible with upper and lower dentitions on both sides (UM F4-305). Upper Calcaire de Fons (early Ludian); Fons 4, Gard, France.

RANGE. Marinesian, England; Marinesian to early late Ludian, France; and early to early late Ludian, Switzerland.

MATERIAL. Two left P^3s (M36392, M36426); three left M^1s (M35390, M35608, M37090); right M^1 (M37091); three left M^2s (M35601–3); four right M^2s (M35600, M35604, M35606, M37092); three right M^3s (M35609, M37093–4); twelve $M^{1/2/3}$ fragments (M35607, M35610–1, M35630, M35713–4, M36395, M37095–8, M37111); right $P_{2/3}$ (M37099); left M_1 (M35612); right M_4 talonid fragment (M35617); fifteen $M_{1/2/3}$ talonid fragments (M35391, M35397–9, M35620–6, M37105–8) and twenty lower molar trigonid fragments (M35392–6, M35613–6, M35618–9, M35627–9, M37100–4, M37109).

DOUBTFULLY REFERRED SPECIMEN. Edentulous left mandibular fragment with distal M_4 alveolus (M37571).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. See Crochet (1979: 372).

DESCRIPTION. This species is much larger than and easily distinguished from *A.* aff *goethei* at Creechbarrow. Crochet (1980: 105–110) described French post-Bartonian assemblages in detail. Because of the apparent geographical and/or stratigraphical variation involved, variation in the Creechbarrow assemblage is documented here. Measurements are given in Tab. 2.

M^1: On two specimens, cusp C is quite large, only slightly smaller than, and well separated from, D. On two others (e.g. Pl. 3, fig. 7) it is slightly to much smaller, and very close to D. In the former there is little or no ectoflexus but it deepens asymmetrically with increasing reduction in size of cusp C. Cusp B is fairly constant in size, slightly larger than D, and in two specimens it has a strong distal crest (Pl. 3, fig. 7). Width of the stylar shelf at cusp C is fairly constant at about $\frac{1}{3}$ of its width at the metacone. There is a distinct postflexus in two out of three specimens and the protocone lobe is constantly angular lingually. The length of the protocone lobe varies from a little less to a little more than half the tooth length.

M^2: Cusp C remains in a central position but varies a little in size. B, C and D are subequal, although either B or D tends to dominate slightly. One fragmentary specimen (M35606) has a twinned cusp C, as often occurs in the probable ancestral species *A. bastburgense.* The depth of the ectoflexus varies from non-existent to shallow, depending on the size of cusp C. Two out of six specimens have a distal crest to cusp B (including M35606). The width of the stylar shelf is fairly constant and as on M^1. Presence and depth of a postflexus varies considerably and is most accentuated on M35602. Lingual angularity appears fairly constant as in M^1, although abrasion often makes it difficult to judge; it is reduced in the specimen with the longest protocone lobe (M37092). Length of the protocone lobe varies from about $\frac{1}{2}$ to $\frac{2}{3}$ of the tooth length.

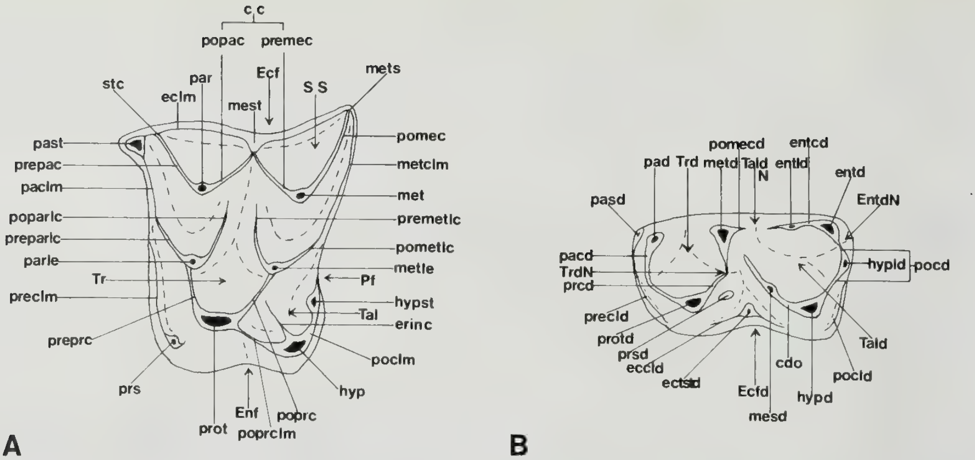
M^3: In M37093, regularly spaced cusps B, C and D decrease slightly in size in that order. A fragmentary specimen shows the same size relationship between C and D, but both are smaller than on M37093. In both the ectoflexus is shallow. Only M37093 is well enough preserved to show the other features (see Pl. 3, fig. 9).

M_1: The holotype M_1 is broken lingually but appears to have a slightly longer talonid relative to the trigonid than the only complete Creechbarrow lower molar (Pl. 3, fig. 10).

M_4: This talonid fragment is very narrow compared to the $M_{1\quad 3}$ talonids (Pl. 3, fig. 12).

Mandible: This edentulous fragment retains parts of the gently sloping leading edge of the ascending ramus, the inflected angular process and the large dental foramen typical of didelphids. Size suggests that it may belong to this species.

DISCUSSION. Of the characters which Crochet (1980: 109–110) found to vary between assemblages from the localities Fons 4 and La Bouffie on the one hand and Les Pradigues and Lavergne on the other, only one can be shown to be fairly constant at Creechbarrow, the lingual angularity of the upper molar protocone lobe. These results could be used to support either of his hypotheses: i.e. that the species is polytypic or that two parallel lineages developed (in the Ludian). The relatively small number of specimens from all localities suggests that the extent of the morphological intraspecific variation has not yet been adequately sampled.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Text-figure 8 Dental nomenclature of primitive eutherian quadritubercular cheek teeth. Based mainly on Van Valen (1966: text-fig. 1) and Szalay (1969: text-fig. 1). A, Left upper molar. Buccal edge towards top of page, lingual towards bottom. B, Left lower molar. Buccal edge towards bottom of page, lingual towards top.

Abbreviations:

A. cc—centrocrista
Ecf—ectoflexus
eclm—ectocingulum
Enf—entoflexus
erinc—'erinaceid crest'
hyp—hypocone
hypst—hypostyle
mest—mesostyle
met—metacone
metclm—metacingulum
metle—metaconule
mets—metastyle
paclm – paracingulum
par—paracone
parle—paraconule
past—parastyle
Pf—postflexus (new term)
poclm—postcingulum
pomec—postmetacrista
pometlc—postmetaconule crista
popac—postparacrista
poparlc—postparaconule crista
poprclm—postprotocingulum
poprc—postprotocrista (= *Nannopithex* fold)
preclm—precingulum
premec—premetacrista
premetlc—premetaconule crista
prepac—preparacrista
preparlc—preparaconule crista
preprc—preprotocrista
prot—protocone
prs—protostyle
SS—stylar shelf
stc—stylocone
Tal—talon basin
Tr—trigon basin

B. cdo—cristid obliqua
eccld—ectocingulid
Ecfd—ectoflexid
ectstd—ectostylid
entcd—entocristid
entd—entoconid
EntdN—entoconid notch
entld—entoconulid
hypd—hypoconid
hypld—hypoconulid
mesd—mesoconid
metd—metaconid
pacd—paracristid
pad—paraconid
pasd—parastylid
pocd—postcristid
pocld—postcingulid
pomecd—postmetacristid
prcd—protocristid
precld—precingulid
protd—protoconid
prsd—protostylid
Tald—talonid basin
TaldN—talonid notch
Trd—trigonid basin
TrdN—trigonid notch

Infraclass **EUTHERIA** Gill 1872

Order **PROTEUTHERIA** Romer 1966 (*sensu* Sigé 1975)

Family **PANTOLESTIDAE** Cope 1884 (*sensu* Van Valen 1967)

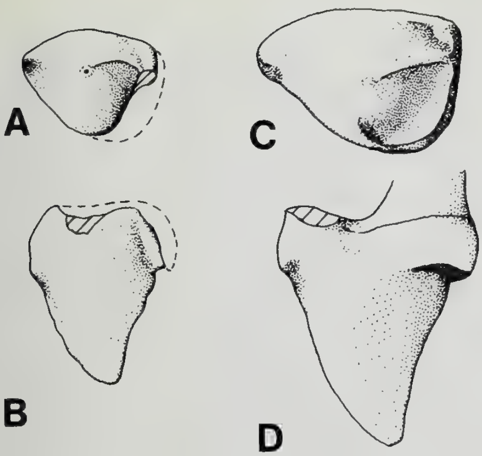
Cray (1973: 48) listed genera in this family up to that time. Subsequently Van Valen (1978) has synonymized *Pantomimus* with the arctocyonid condylarth *Prothryptacodon* and Heissig (1977) has synonymized *Opsiclaenodon* Butler 1947 and *Androconus* Quinet 1965 with *Cryptopithecus* Schlosser 1890. Further complications and problems with Palaeocene genera are discussed by Dorr (1977).

? **Pantolestidae**, gen. et sp. indet.
(Text-fig. 9A–B)

MATERIAL. Left $P^{1/2}$? fragment (M36435); two left $P^{2/3}$ fragments (M36390, M37407).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. $P^{1/2}$?: This single-cusped tooth, broken basally, is identified tentatively as it is smaller than those identified as $P^{2/3}$. Its curved cusp indicates it is not a lower tooth.



Text-figure 9 A–B, Pantolestidae indet. from Creechbarrow. Occlusal and buccal views respectively of left $P^{2/3}$ (M36390). C–D, *Cryptopithecus major* (Lydekker) from the Lower Headon Beds, Hordle Cliff. Occlusal and buccal views respectively of left $P^{2/3}$ (M34756). All × 8.

$P^{2/3}$: An upper tooth from Hordle Cliff (M34756; Text-fig. 9C–D) compares well in morphology with those of *Cryptopithecus sideroolithicus* Schlosser 1890, identified by Heissig (1977: 216, figs 6–8) as P^3 and P^4. It seems likely that the latter are really P^2 and P^3, as two teeth from Hordle Cliff, with morphology typical of that of a pantolestid P^4, are present in the BM(NH) collections. These are broader with a distinct protocone and are considered to belong to *Cryptopithecus major* (Lydekker 1887) Heissig 1977. Two teeth from Creechbarrow closely resemble M34756 but are slightly smaller. The better preserved (M36390) has a weaker parastyle which is situated higher on the crown and the preparacrista extends further apically. The distal and distolingual regions are missing in both teeth.

Order **LIPOTYPHLA** Haeckel 1866
(rank emend. Gregory 1910)

Insectivore classification has had a chequered history (see Butler 1972). Certain fossil and modern groups that at one time or another have been included peripherally in the Insectivora are generally now given ordinal status of their own (e.g. Apatotheria, p. 327, and Proteutheria, p. 222). For the rest Butler (1972) advocated the use of a restricted insectivore order, using Haeckel's (1866) name Lipotyphla, for the extant erinaceids, talpids, soricids, solenodontids, tenrecids and chrysochlorids and several extinct families. Novacek (1976) preferred to use the order Insectivora in a restricted sense for the Lipotyphla. The name Lipotyphla has the advantage of being narrower in its range of meaning than Insectivora. Butler (1972: 255) listed six important characters common to this group: 1, absence of caecum; 2, reduction of jugal; 3, expansion of maxilla in orbital wall, displacing palatine; 4, mobile proboscis moved by a series of muscles which influence the form of the skull; 5, reduced pubic symphysis; 6, haemochorial placenta. Characters 2–5 are the most likely to be useful in the fossil record and only 2–4 have been recognized in the early Tertiary. Moreover, skulls are rare and further extrapolation is by means of the teeth.

Suborder **ERINACEOMORPHA** Saban 1954 (*sensu* Sigé 1976)

Family **AMPHILEMURIDAE** Heller 1935

Type genus. *Amphilemur* Heller 1935 (including *Alsaticopithecus* Hürzeler 1947*b*). The synonymy of Russell *et al.* (1975) is upheld against Koenigswald & Storch's (1983) claimed distinctions between *Amphilemur* and *Alsaticopithecus*, which I cannot substantiate.

Included genera. *Gesneropithex* Hürzeler 1946 (including *Anchomomys* Stehlin 1916 in part) and *Pholidocercus* Koenigswald & Storch 1983.

RANGE. Lutetian to Ludian, Europe.

EMENDED DIAGNOSIS (modified from Koenigswald & Storch 1983). Dental formula $\frac{3\ 1\ 4\ 3}{3\ 1\ 4\ 3}$. $I\frac{1}{1}$–$P\frac{3}{3}$ of approximately equal size, although C^1 may be rather larger and P^1 rather smaller. Thus relatively little differentiation of the antemolar dentition, although sharp size and complexity change from $P\frac{3}{3}$ to $P\frac{4}{4}$. Lower teeth mesial to P_4 single-rooted and bladelike, and becoming progressively procumbent and overlapping forwards. $P\frac{4}{4}$ premolariform. P^4 essentially without metacone; P_4 *with* unicuspid talonid or with very small entoconid and *distinct cristid bisecting the distal protoconid slope and extending for the length of the talonid basin.* Molars relatively bunodont with rather inflated main cusps. $M\frac{1}{1}$ tend to be slightly longer than $M\frac{2}{2}$. *Upper molars with* buccal angles blunt, *a mesostyle at least on* M^3, narrow stylar shelves and well developed paraconule and metaconule with weak cristae. $M^{1\ 2}$ quadrate, essentially as long as broad, *with postmetacrista short and weak*; *paracone and metacone* low and buccal and *better separated from each other than metacone and paracone of successive teeth*; hypocone medium to large, conical; erinaceid crest may be present. *Lower molars with* mesiodistally compressed trigonid, low transverse *paracristid* without paraconid *which does not reach lingual margin*; *broadly rounded talonid basin*; little height distinction between trigonid and talonid; talonid wider than trigonid at least on $M_{1\ 2}$; *hypoconid higher than entoconid*; cristid obliqua contacts distal trogonid wall below and buccal to the base of the protoconid–metaconid notch; entoconulid present; wear moderately transverse (*c.* 30°–40° to crown base) and normally penetrates no lower than buccal cingulum. M_{1-2} *hypoconulid* just lingual to midline, *separated from postcristid by distal grooves. Protoconid lower than metaconid on* $M_{2\ 3}$, subequal on M_1. *Mental foramina occur below* P_2, below P_4/M_1 and sometimes below P_3. Dermal ossification of tail known in one genus.

DISCUSSION. Koenigswald & Storch (1983) have recently provided compelling dental and postcranial evidence, from four skeletons of *Pholidocercus* from the Lutetian of Messel, W. Germany, which places this family in the Lipotyphla rather than the Primates, where it has frequently been classified in the past. I (Hooker 1982) independently came to the same conclusion, on the basis of cranial and dental remains of *Gesneropithex* from the Bartonian and Ludian of the Hampshire and Paris Basins. Koenigswald & Storch (1983) included in the family the poorly known type species of *Gesneropithex* but excluded other species that are referred to it herein. Inclusion of the latter, which considerably expand our knowledge of the genus, requires certain changes to the family diagnosis: e.g. size does not always decrease continuously from $M\frac{1}{1}$ to $M\frac{3}{3}$, one species showing much intraspecific size variation in $M\frac{3}{3}$. Those characters in the diagnosis which are italicized are unique to the Amphilemuridae and distinguish them from the other erinaceomorph families Adapisoricidae, Erinaceidae and Nyctitheriidae. Other characters distinguish them from only one or two of these families, but until the relationships within the Erinaceomorpha are better known the diagnosis cannot be made more precise. Comparison with the diagnosis of Russell *et al.* (1975) of the Adapisoricidae shows relatively few differences from that of the Amphilemuridae. In fact separation of the two leaves the Adapisoricidae based only on primitive characters. A possible solution to this problem may be a more detailed breakdown of the Adapisoricidae into smaller family units. This has already begun (Bown & Schankler 1982; Gingerich 1983, at subfamily level; Novack *et al.* 1985).

Genus *GESNEROPITHEX* Hürzeler 1946

TYPE SPECIES. *G. peyeri* Hürzeler 1946. Ludian fissure filling; Gösgen Pumpstation, Canton Solothurn, Switzerland.

INCLUDED SPECIES. *G. latidens* (Teilhard 1921) comb. nov.; *G. grisollensis* (Louis & Sudre 1975) comb. nov.; *G. figularis* sp. nov.; and *G.* sp. indet. (from Robiac; Sudre 1969*a*,*b*).

RANGE. Auversian to Ludian. England, France and Switzerland.

EMENDED DIAGNOSIS. Upper incisors, canine and $P^{1/2}$ with prominent distal cusp. Lower anterior teeth strongly procumbent. C_1 without talonid cusp. P^2 relatively narrow. P^3 with small protocone and parastyle. P^4 approximately as long as broad with prominent parastyle. P_4 with subequal metaconid and protostylid both much smaller than protoconid; paraconid median. M^{1-2} essentially square in outline, hypocone as far from protocone as metacone is from paracone. Lower molars with paracristid far from lingual edge and without enamel wrinkling.

Differential diagnosis. *Amphilemur* and *Pholidocercus* have the upper teeth in front of P^3 with weaker distal cusp; anterior premolars with lower length : width ratio; stronger upper molar mesostyles, M^{1-2} more trapezoidal with smaller hypocones closer to protocones; and P_4 without protostylid.

Amphilemur has P_4 with a larger metaconid and more lingual paracristid.

Pholidocercus has lower teeth in front of P_4 less procumbent; C_1 with talonid cusp; P^3 without paracone or parastyle; P^4 relatively shorter with smaller parastyle; P_4 with shorter talonid; and lower molars with paracristids extending further lingually and more concave talonid basins with enamel wrinkling.

Note that *Gesneropithex* and *Amphilemur* are known mainly from teeth and it is not known whether either were like *Pholidocercus* in the postcranial skeleton or presence of dermal ossification.

Taxonomic history. The treatment of species herein referred to *Gesneropithex* by authors is given below in chronological order. Koenigswald & Storch (1983) have comprehensively dealt with other members of the family in a similar way.

Teilhard (1921) described *Anchomomys latidens*, but the generic assignment was provisional. The adapid *Anchomomys* was then considered a tarsiid.

Hürzeler (1946, 1947*a*) described *Gesneropithex peyeri* as a primate in Prosimii, *incertae sedis*.

Simons (1962, 1963) and Crusafont-Pairo (1967) placed *Gesneropithex* in the Adapidae.

Russell *et al.* (1967: 40) placed *Gesneropithex* provisionally in the Adapidae.

Sudre (1969*a*) figured an M^1 and DP^4 from Robiac as *Dichobune* sp., an artiodactyl.

Sudre (1969*b*) figured a mandibular fragment with M_{2-3} from Robiac as *Gesneropithex* sp.

Szalay (1971*b*) considered *Gesneropithex* an adapisoricid.

Szalay (1974) considered '*Anchomomys*' *latidens* neither a close relative of *Anchomomys*, nor an adapid, nor a primate, but believed it to be an erinaceid insectivoran.

Russell *et al.* (1975) synonymized *Alsaticopithecus* with *Amphilemur*, placing it in the family Amphilemuridae as Primates *incertae sedis*. They also selected the mandibular fragment (NMB GP128) as lectotype of *Gesneropithex peyeri* which they considered was not an adapisoricid, but did not suggest what it could be. The paralectotype M^2 (NMB GP127) they reidentified as *Amphilemur* sp.

Louis & Sudre (1975) described a new species which they placed in '*Anchomomys*' ('*A.*' *grisollensis*) in ? Adapidae. They figured a probable DP^4 as a DP^3 and a DP^4 of *Microchoerus* or *Necrolemur* (cf. Schmidt-Kittler 1977*a*: fig. 10 for *Microchoerus* DP^4) as a DP^4 of '*A.*' *grisollensis*. They considered the new species related to '*A.*' *latidens*, neither being true *Anchomomys* and together probably with *A. pygmaeus* (Rütimeyer 1890) (now a *Periconodon*, see Gingerich, 1977*a*) belonging to a primate group of as yet uncertain affinities.

Hooker (1977*b*) recorded *Gesneropithex* from Creechbarrow.

Kay & Cartmill (1977: 36) showed that the interorbital index of 'the erinaceoid "*A.*" *latidens*' plotted well within the insectivores especially the tupaiids, but also alongside the microsyopid primate *Palaechthon*.

Sudre (1978*b*) reidentified the M^1 and DP^4, previously (1969*a*) identified as *Dichobune* sp., as *Mouillacitherium* aff. *elegans*, another dichobunid artiodactyl.

Hooker & Insole (1980) reidentified the Creechbarrow *Gesneropithex* as *Amphilemur* sp. 1.

Koenigswald & Storch (1983) included *Gesneropithex peyeri* in the Amphilemuridae but excluded '*Anchomomys*' *grisollensis*.

Recent contributions. Two recent contrasting classifications of *Gesneropithex* are those of Szalay (1971*b*) and Russell *et al.* (1975), who also discuss *Amphilemur* in the same context. New material from Creechbarrow described here as *Gesneropithex figularis* and from Hordle Cliff identified here as *Gesneropithex* aff. *grisollensis* (Louis & Sudre 1975) has an important bearing on their contrasting views. In the light of this material, the views of Szalay and Russell *et al.* will be considered in detail.

Szalay's (1971*b*) reasons for removing *Gesneropithex* from the Primates and reclassifying it in the '*Adapisorex*-like erinaceotans' were:

1. Shallower mandible than any early Tertiary primate.
2. P_4 unique if primate – narrow crown, mesial position of paraconid and large talonid unlike any adapid, anaptomorphid, microchoerid or early cercopithecid. Total complex of characters in P_4 compatible with *Adapisorex gaudryi*.
3. Distal border of talonid of lower molars barely rounded, and postcristid between prominent entoconid and hypoconid nearly straight when viewed in horizontal plane.
4. Tiny, centrally placed (molar) hypoconulid is deep in groove between entoconid and hypoconid.
5. (Molar) trigonid relatively erect, unlike the slightly procumbent talonid (=trigonid?) of adapids, microchoerids or anaptomorphids.
6. Upper molar lacks parastyle and metastyle and the nature of the cuspidate hypocone indicates that the genus most likely does not share homologous advanced similarities with upper molars of early Tertiary primates.
7. $M^{2?}$ is similar in position and conformation of hypocone to such erinaceotans as *A. gaudryi*, *Macrocranion tupaiodon* and *Galerix exilis*.

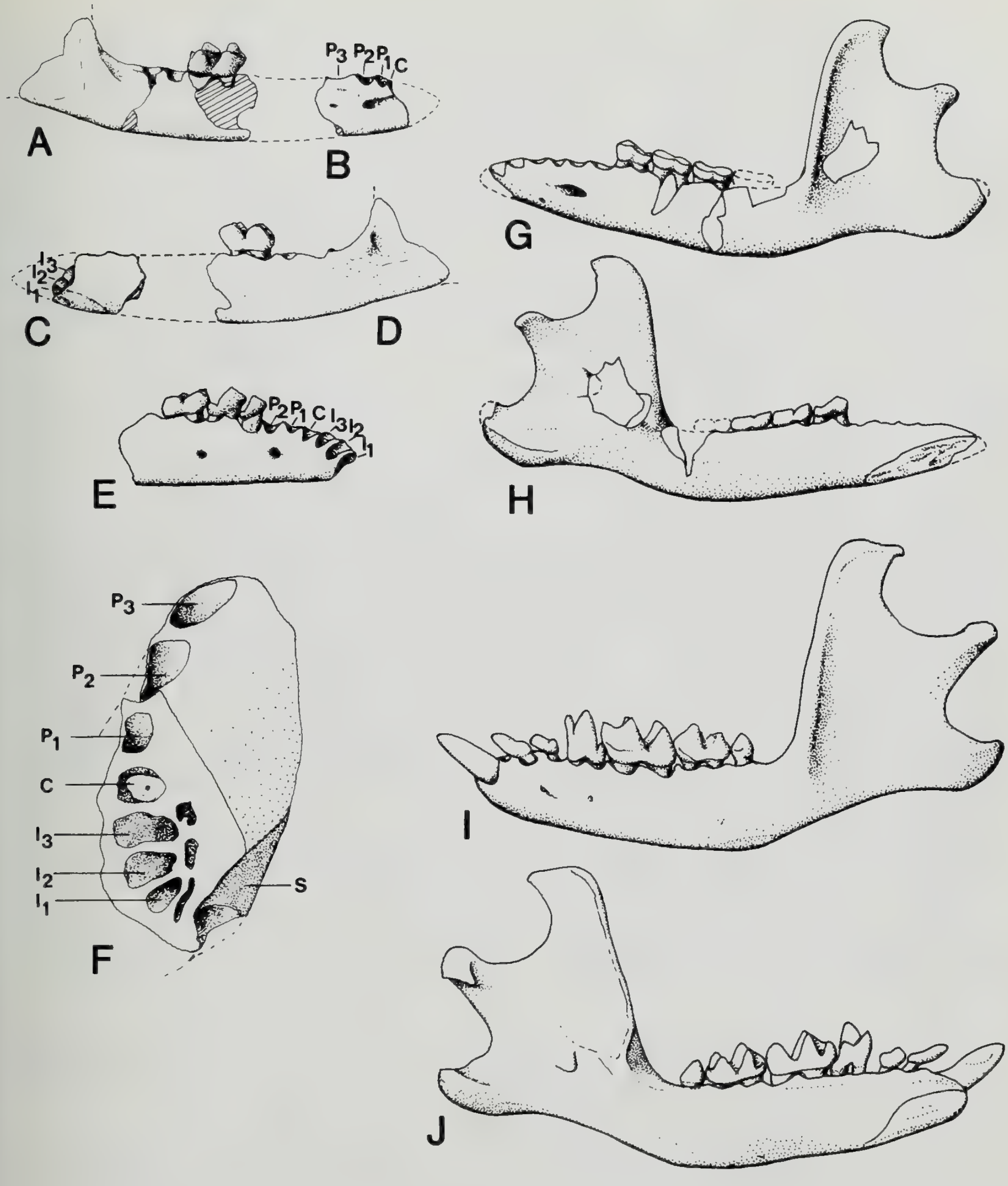
Russell *et al.* (1975: 171–172) admitted that *G. peyeri* P_4–M_2 showed many adapisoricid characters. They dismissed Szalay's (1971*b*) arguments for transfer of *Gesneropithex* to the erinaceoids by equating them with those that they used to return *Amphilemur* to the Primates. They (1975: 172) repeated some of the distinctions from the Adapisoricidae that they had already made for *Amphilemur* (1975: 170–171), but did not suggest relationships with this genus. They stated (1975: 171) that some specimens of the primates *Pelycodus*, *Hemiacodon* or *Omomys* have a mandible shallower than in *Amphilemur* (*Gesneropithex* has a mandible of similar depth). They suggested homologies for the four and a half alveoli mesial to P_4 which Szalay had ignored, and considered that the most mesial, also being the largest, had housed the canine and was thus unlike an adapisoricid. Koenigswald & Storch (1983: 473–474) reinterpreted these alveoli as single-rooted P_3–I_2.

Szalay's arguments were mainly concerned with removing *Gesneropithex* from the Primates, whereas the arguments of Russell *et al.* served only to remove it from the Adapisoricidae, without suggesting what it could be. The latters' reasons why *Amphilemur* was not an adapisoricid are of direct relevance and are listed below:

1. Either I_1 or lower canine missing makes the dentition atypical for the Adapisoricidae which have $\frac{?3\ 1\ 4\ 3}{3\ 1\ 4\ 3}$.
2. Molar paraconid only projects forwards a little on M_2, is central and closely hugs the metaconid.
3. Metaconid is high (compared to protoconid) on M_2.
4. Hypoconid instead of entoconid is highest of the talonid cusps.
5. P_4 and molars swollen and with broad talonid.

New discoveries. The new material provides an answer to two points raised above: the dental formula (point 1 of Russell *et al.* above), and the jaw depth (Szalay's point 1 above).

Dental formula. Two mandibular rami identified as *G.* aff. *grisollensis* from the Hordle Cliff Mammal Bed are complete to the very front. One shows seven alveoli in front of P_4; the other shows six alveoli in front of P_3 which itself has fused mesial and distal roots occupying a single alveolus (see Text-fig. 10E and G). The six teeth preserved in front of P_4 in *A. eocaenicus* are all single-rooted, and isolated teeth of almost identical morphology have also been recovered at Creechbarrow and from the Hordle Cliff Mammal Bed. Thus the most anterior alveolus in the



Text-figure 10 A–D, F, *Gesneropithex figularis* sp. nov. from Creechbarrow. A, D, lateral and medial views respectively of right posterior mandibular fragment with M_2 (M35407). B, C, F, lateral, medial and anteromedial views respectively of right anterior mandibular fragment (M37406). E, *Gesneropithex* aff. *grisollensis* (Louis & Sudre) from the Hordle Cliff Mammal Bed; lateral view of right mandibular fragment with P_3–M_1 (M50199). Alveoli are labelled; S = symphysis. G–H, lateral and medial views respectively of almost complete left mandibular ramus of *Gesneropithex* aff. *grisollensis* from the Hordle Cliff Mammal Bed (M50198). It shows P_4–M_2 and alveoli for I_1–P_3 and M_3. I–J, lateral and medial views respectively of left mandibular ramus of Recent hedgehog, *Erinaceus europaeus* Linné. A–E, G–J × 2; F × 6·6.

Hordle Cliff jaws must have contained an I_1. This conforms with Koenigswald & Storch's (1983) interpretation of *Amphilemur eocaenicus* as having possessed an I_1 and also the undoubted presence of this tooth in *Pholidocercus*. There is thus no support from the dental formula for reference of *Gesneropithex* to the Primates. The only primate with three incisors (*Purgatorius*) already shows some heterodonty here, unlike amphilemurids (Kielan-Jaworowska *et al.* 1979: 250). Several teeth from Creechbarrow closely resemble the tooth identified as I_2 (by comparison with the anteriormost tooth preserved in the jaw of *A. eocaenicus*) but differ in being broader and having a less oblique shape. These are herein tentatively identified as the elusive I_1. The Creechbarrow edentulous anterior mandibular fragment can be matched up with the Hordle Cliff jaws and the alveoli identified as I_1–P_3. Erosion at the front of the jaw means that only the deep recesses of the alveoli still remain (Text-fig. 10B, C and F).

Jaw depth. One of the two mandibular rami from Hordle Cliff mentioned above (M50198) is essentially complete (Text-fig. 10G–H). It was collected broken during sieving and skilfully mended by the collector Mr R. Gardner. P_4–M_2 are present but quite heavily worn. The horizontal ramus is shallow like *A. eocaenicus* and *G. peyeri* and the ascending ramus shows a striking resemblance to that of the modern hedgehog *Erinaceus europaeus* L. (see Text-fig. 10I–J). When tracings of the posterior horizontal and ascending rami of a range of early Tertiary and modern prosimian primates are superimposed on that of *G.* aff. *grisollensis*, with the bases of the tooth rows aligned, the primate ascending rami are not bent upwards and lie posterior and ventral to that of *Gesneropithex* (e.g. Text-fig. 11E). (Szalay & Delson's (1979: 50, fig. 17E–F) figure of a reconstructed *Palenochtha* jaw closely resembles an erinaceomorph in the characters mentioned above; however, study of the material of this genus in the UMMP shows it to be like other plesiadapiform primates and unlike erinaceomorphs.) The same is true for those prosimians with shallow as with deep jaws. It is probable that the rotation in primates was necessary to move the ascending rami backwards away from the enlarging eyes. The ascending ramus of most modern lipotyphlans and of known adapisoricids is like that of *Gesneropithex* in orientation. It is evident that the difference of opinion on jaw depth between Szalay (1971*b*) and Russell *et al.* (1975) is partly a question of definition. Although not necessarily shallower below the tooth row than in a primate, the upward bending of the ramus more posteriorly in *Gesneropithex* gives it a shallower appearance in this region, especially when the coronoid process is mainly broken away.

Thus both dental formula and jaw shape in *Gesneropithex* are dissimilar from primates and similar to adapisoricids. This supports Szalay's (1971*b*) conclusions and removes the first objection of Russell *et al.* (1975) to the inclusion of *Amphilemur* in the Adapisoricidae.

OTHER EVIDENCE. **Cranium.** An examination of the unique holotype cranium of *G. latidens* (MNHN Qu11012) from the Phosphorites du Quercy (exact horizon and locality unknown) provides further relevant characters (see Text-fig. 11A–C). The following are typical of lipotyphlans:

1. Extensive preorbital depression extending posteriorly right to orbit which has sharp laterally projecting anterior edge for accommodation and attachment of nasolabial muscles (see Butler 1956).
2. Lacrymal foramen inside orbit (as in *Macrocranion*, see Maier, 1979: 43).
3. When the complete mandibular ramus of *G.* aff. *grisollensis* from Hordle Cliff is occluded with the cranium of *G. latidens* (the two are very closely related if not conspecific) the distance between the anterior edges of the orbit and the ascending ramus leaves room for only a small eye.

In addition, the infraorbital foramen is large. This excludes most primates except for the earliest genus known from cranial remains – *Palaechthon* (see Kay & Cartmill 1977), where the infraorbital foramen is also large. There are, however, no other special similarities between *Gesneropithex* and *Palaechthon*.

Some striking similarities can, however, be observed between *Gesneropithex* and the modern galericine erinaceids *Hylomys*, *Neotetracus* and *Podogymnura*. In these genera and in tupaiids, however, the position of the orbit and infraorbital foramen vary considerably (see Table 3).

Table 3 Variation in position of orbit and infraorbital foramen in *Gesneropithex latidens* and other species.

Species	Position of infraorbital foramen	Position of anterior orbital edge
Gesneropithex latidens	P^4 middle	M^2 paracone
Macrocranion tupaiodon	P^3 distal edge	M^2 paracone
Palaechthon nacimienti	P^3 middle	M^1 paracone
Hylomys suillus	P^4 parastyle	M^1 paracone
Neotetracus sinensis	P^4 parastyle	M^1 paracone
Podogymnura truei	M^1 middle	M^2 paracone
Echinosorex gymnurus	P^4/M^1 junction	M^1 distal half
Tupaia glis	P^3 distal edge	M^1 mesial edge
Anathana elliotti	P^2 distal edge	P^4 parastyle
Urogale cylindrura	P^3 middle	M^2 middle
Dendrogale melanura	P^3 middle	M^1 middle
Ptilocercus lowi	P^4 middle	P^4 middle

Hylomys, *Neotetracus* and *Podogymnura* have a depression for the nasolabial muscles but only in *Hylomys* and *Neotetracus* has this a dorsal limiting ridge as in *Gesneropithex*. The orbit, as reconstructed in Text-fig. 11B, is more like *Podogymnura* than the other genera in position, size and apparent weakness of the dorsal edge. The irregular grooves on the frontal region of *Gesneropithex* are very similar in scale and pattern to *Neotetracus* and *Hylomys*; in contrast they are more anastomosing in *Podogymnura*.

The unique cranium of *G. latidens* is considerably distorted. It has been shortened, with the anterior region of the parietals having been sheared to form an imbricate structure. The right frontal has also been pushed anteroventrally to slide beneath the dorsal edge of the right maxilla, reducing the angle between the two, reducing the overall height of the cranium in this region and further shortening the whole cranium. In the reconstruction of the skull of *Gesneropithex*, an attempt has been made to reverse these processes. It is probable that the structural displacements which have taken place diagenetically were at sutures. The only ones visible on the specimen are those delimiting part of the lacrymal and maxilla (Text-fig. 11C). There is no suggestion of a jugal having a facial or orbital extension. The absence of this extension is a diagnostic lipotyphlan character but although the jugal has a facial extension in the tupaiids (Order Scandentia), the sutures are often completely fused and invisible. Maier (1979: 43) stated that in *Macrocranion* 'a slender process of the zygomatic (= jugal) forms the lower border of the orbit nearly reaching the lacrimal region; this is a feature more typical of the menotyphlan insectivores than of lipotyphla'; but the suture is not obvious from his figure (1979: 44, fig. 4).

The orbit of *G. latidens*, now mainly cleaned of matrix by Dr D. E. Russell, shows the presence of a lacrymal foramen and below it the much larger opening of the infraorbital canal; the arrangement is most like *Podogymnura* (see Text-fig. 11C–D) among modern galericines. See also Butler (1956: fig. 7) for orbital bones of *Echinosorex* and contrasting insectivores.

The back of the cranium has a prominent occipital crest, unlike *Hylomys*, *Neotetracus* or *Podogymnura* but more like the larger *Echinosorex* (Text-fig. 11A–B).

Teeth. The most relevant features of the teeth in the Amphilemuridae are compared with the early Tertiary prosimians and the Adapisoricidae in Table 4. They further support Szalay's (1971*b*) views on the erinaceoid relationships of *Gesneropithex* and indicate that the Amphilemuridae should not be included in the Order Primates.

The characters 2–5 of Russell *et al.* (1975), listed on p. 226 as reasons why *Amphilemur* is not an adapisoricid, will now be considered. The P_4 and lower molars seem to be no more swollen and to have talenids no broader than those of some adapisoricids. The reduction of the lower molar paracristid (paraconid absent) is associated with increase in size of the upper molar

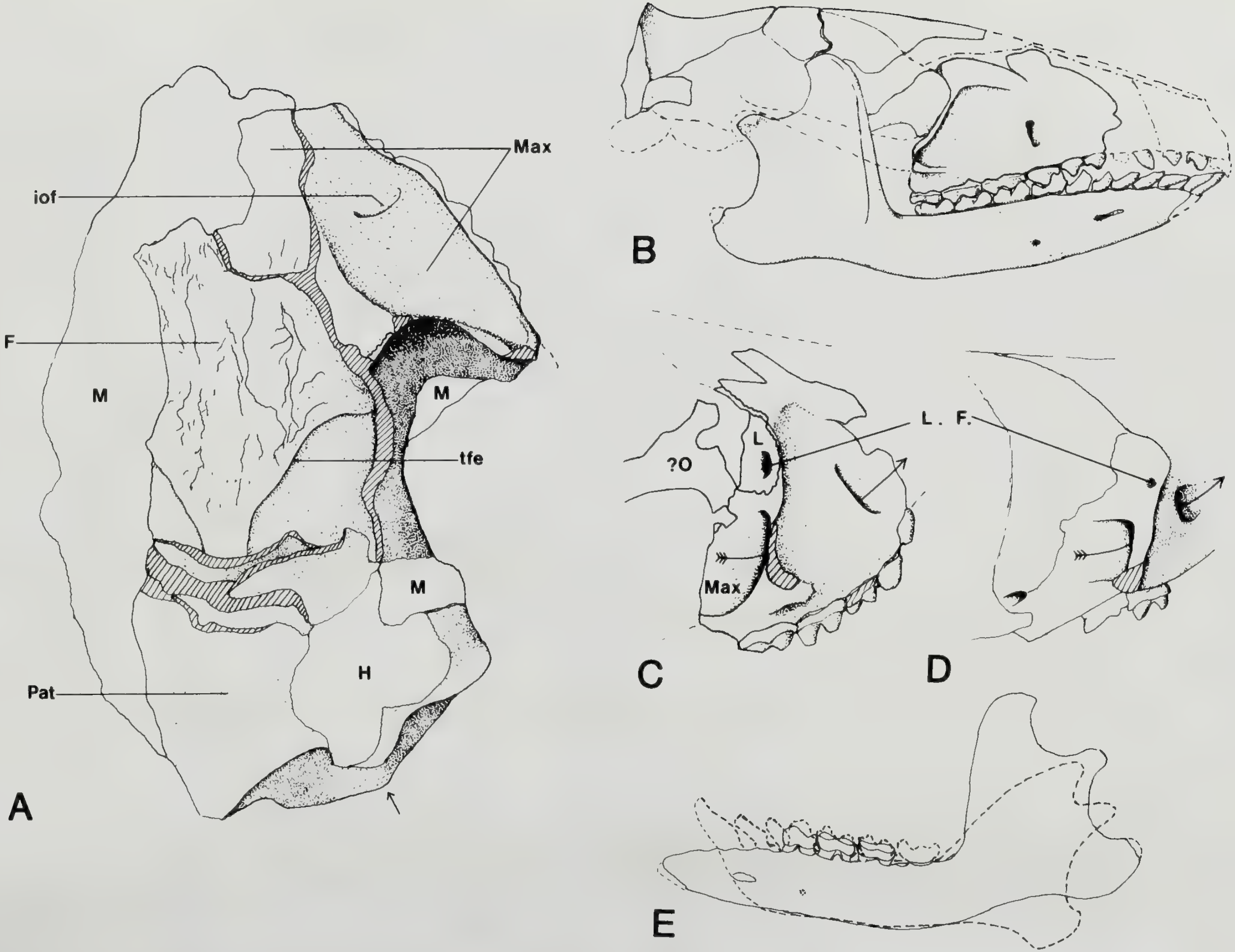

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Table 4 Features of the teeth of Amphilemuridae compared with early Tertiary prosimians and Adapisoricidae.

Character	Early Tertiary prosimians	Amphilemuridae	Adapisoricidae
Tendency to develop *Nannopithex* fold	yes	no	no
Tendency to develop 'erinaceid' crest	no	yes	yes
M_3 talonid and hypoconulid	expanded	reduced	reduced
Presence of molar paraconid	yes	no	sometimes
Position of molar protoconid re metaconid	mesiobuccal	buccal	buccal on M_{2-3} mesiobuccal on M_1
Anterior lower teeth	heterodont, canine or incisor enlarged, other teeth upright or, if procumbent, broad	homodont, procumbent, blade-like	homodont, procumbent, blade-like where known (e.g. *Macrocranion*, see Tobien 1962; *Litolestes*, see Schwartz & Krishtalka 1976)

hypocone and more transverse shear between the teeth. The increase in height of the lower molar hypoconid is associated with the greater separation of the upper molar paracone and metacone. The lower molar metaconid is the same height as the entoconid as in adapisoricids; therefore the protoconid must have reduced in size. This is likely to be related to the reduction of the upper molar metastyle causing the metacone of one tooth to lie nearer to the paracone of the following tooth. These modifications are typical of mammals whose teeth have attained the quadritubercular state, as for instance has happened independently in ungulates and primates. Most of the other characters of *Amphilemur* and *Gesneropithex* link them strongly with the Adapisoricidae. Those that do not, instead of pointing to relationships with primates, suggest modifications for a less insectivorous, more herbivorous diet, as has already been suggested for *Macrocranion*, a closely related adapisoricid (see Maier 1979).

A possible ancestry of the Amphilemuridae could be sought among the pre-Middle Eocene Adapisoricidae. *Neomatronella* from the European early Eocene is a potential candidate. It shows certain characters in common with the Amphilemuridae like a similarly reduced M_3 talonid; lower molar paracristid not reaching lingual edge; M_{1-2} hypoconulid distinctly

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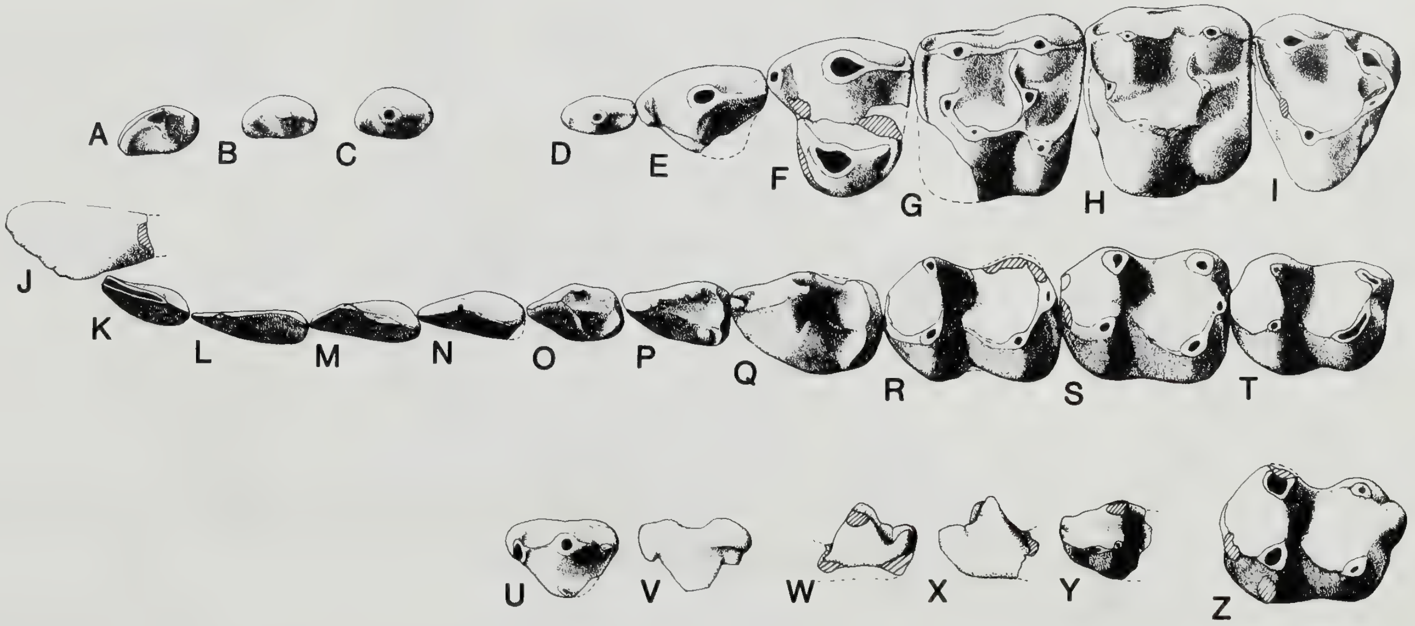
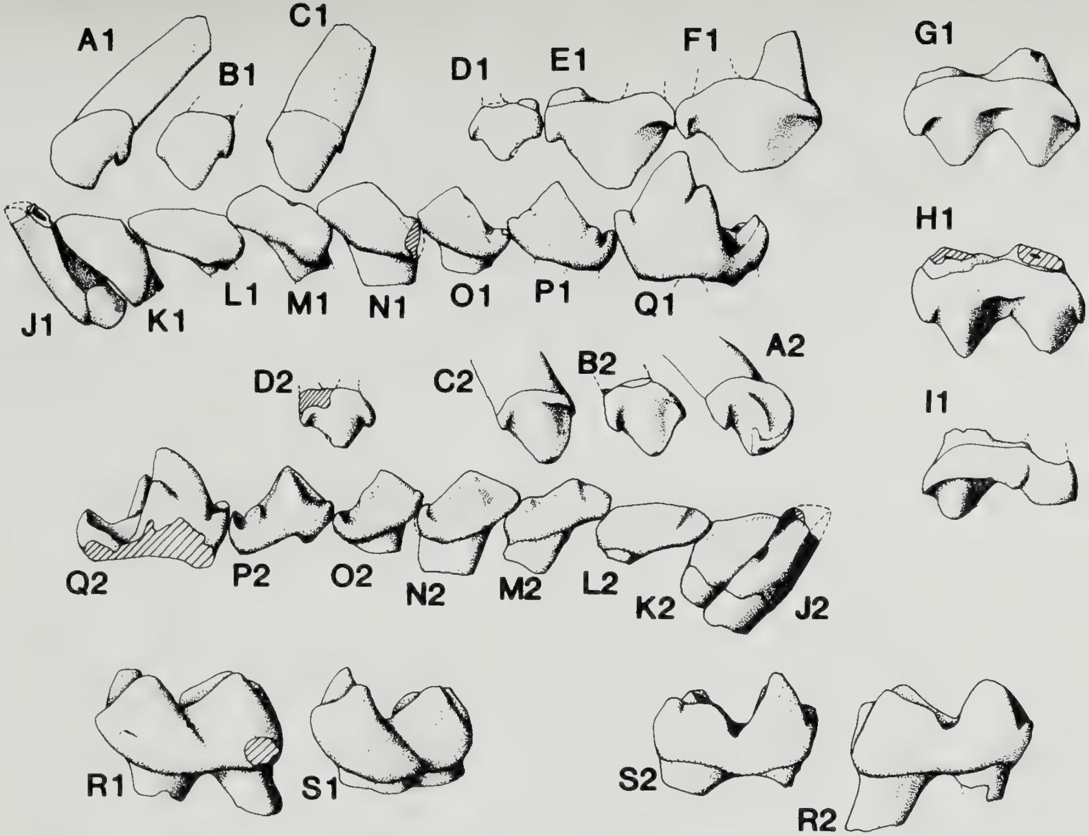
Text-figure 11 A, dorsal view of holotype cranium of *Gesneropithex latidens* (Teilhard) (MNHN Qu11012) from the Phosphorites du Quercy; ×3·3. Abbreviations: M = matrix; H = hole; F = frontal; iof = infraorbital foramen; Max = maxilla; Pat = parietal; tfe = edge of temporal fossa; L = lacrymal; O = orbitosphenoid. Oblique hatching indicates broken surface of bone and arrow the position and orientation of midline of posterior region of cranium. B, reconstruction of *Gesneropithex* skull, based on holotype cranium of *G. latidens* (MNHN Qu11012) and left (reversed) mandibular ramus (M50198) from Hordle Cliff, with addition of teeth of *G. figularis* sp. nov. from Creechbarrow; ×2. C–D, posterolateral views of right orbital regions of crania of *Gesneropithex latidens* (holotype) and Recent *Podogymnura truei* Mearns (BMNH ZD53.660) respectively; ×3·3. L.F. = lacrymal foramen; arrow indicates course of infraorbital canal. E, outlines of mandibular rami of *Gesneropithex* aff. *grisollensis* (Louis & Sudre) (unbroken line) ×2, and of *Pseudoloris parvulus* (Filhol) (broken line) about ×4, superimposed with the cheek tooth rows aligned. *G.* aff. *grisollensis* is based on a specimen from Hordle Cliff (M50198), and *P. parvulus* both on a specimen from Hordle Cliff (M50200) and on MNHN unnumbered from the Phosphorites du Quercy.



Text-figure 12 *Gesneropithex figularis* sp. nov., from Creechbarrow. A–U, Y–Z are occlusal views, V and X buccal views and W lingual view; all × 5·5. A, right I^2? (reversed) (M36227). B, right I^3? (reversed) (M37142). C, left upper canine (M37403). D, left $P^{1/2}$ (M37141). E, left P^3 (M36417). F, left P^4 (M35653). G, right M^1 (reversed) (M35654). H, **holotype** right M^2 (reversed) (M35420). I, left M^3 (M35659). J, left I_1? (M37139). K, right I_2 (reversed) (M35663). L, right I_3 (reversed) (M35666). M, right lower canine (reversed) (M35668). N, left P_1 (M35670). O, left P_2 (M35402). P, left P_3 (M35678). Q, right P_4 (reversed) (M35681). R, left M_1 (M35685). S, right M_2 (reversed) (M35683). T, right M_3 (reversed) (M35410). U–V, right DP^3? (reversed) (M37405). W–Y, right DP_4 (reversed) (M35684). Z, right M_3 (reversed) (M37130).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Text-figure 13 *Gesneropithex figularis* sp. nov., from Creechbarrow. A1–S1 are buccal views, A2–D2, J2–S2 lingual views, all × 5·5. A, right I^2? (reversed) (M36227). B, right I^3? (reversed) (M37142). C, left upper canine (M37403). D, left $P^{1/2}$ (M37141). E, left P^3 (M36417). F, left P^4 (M35653). G, right M^1 (reversed) (M35654). H, **holotype** right M^2 (reversed) (M35420). I, left M^3 (M35659). J, left I_1? (M35660). K, right I_2 (reversed) (M35663). L, right I_3 (reversed) (M35666). M, right lower canine (reversed) (M35668). N, left P_1 (M35670). O, left P_2 (M35402). P, left P_3 (M35678). Q, right P_4 (reversed) (M35681). R, right M_2 (reversed) (M35683). S, right M_3 (reversed) (M35410).

separated from postcristid; and *Amphilemur*-like P_4. In other ways it is a typical adapisoricid but only teeth from P^4_4 – M^3_3 are known (Russell *et al.* 1975).

Gesneropithex figularis sp. nov.
(Text-figs 10A–D, F, 12–14; Table 5)

v. *1977b* *Gesneropithex* sp.; Hooker: 141.
v. *1980* *Amphilemur* sp. 1; Hooker & Insole: 37.

NAME. Latin, 'pertaining to a potter', referring to English China Clays (Wareham) Ltd., whose help and access to Creechbarrow is much appreciated.

HOLOTYPE. Right M^2, M35420.

PARATYPES (100). The edentulous mandibular fragments M35408, M35695 and M37406 and the teeth (one in a jaw fragment M35407) listed in Table 5.

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Large species of *Gesneropithex*, mean length of M^2 = 3·89 mm (range 3·70–4·15 mm). M^1/P^4 area ratio = 1·29–1·65. M^1/M^2 length ratio = *c.* 1·0. M^2 length/width ratio = 0·87. $M^{1\ \ 2}$ mesostyle normally small to absent; ectocingulum weak; paraconule and metaconule cristae normally strong. P^4 without metacone. P^3 length 92–94% of P^4 length.

DIFFERENTIAL DIAGNOSIS. *G. grisollensis* is smaller, having a slightly stronger M^{1-2} ectocingulum and lower P^3/P^4 length ratio.

G. latidens is smaller, has a lower M^1/P^4 area ratio, higher M^1/M^2 length ratio, slightly stronger ectocingulum, small metacone on P^4 and lower P^3/P^4 length ratio.

G. peyeri is slightly smaller, M^2 length/width ratio lower, M^2 mesostyle large, M^2 ectocingulum slightly stronger and paraconule and metaconule cristae weak.

G. sp. indet. (Robiac; Sudre 1969*a*, *b*) may be slightly larger and has weak paraconule and metaconule cristae. See Text-fig. 14 for size comparisons.

DESCRIPTION. There are certain problems in attributing various anterior teeth to this genus and species. The I_2–P_4 have been identified by comparison with Heller (1935: pl. 1) and a cast of the syntype right mandibular ramus of *A. eocaenicus* (GH 7416); note that I_2 was apparently missing when Dr D. E. Russell cast this specimen, and none of the three syntype rami could be located in Halle in 1979. The attempted identification of I_1 has been explained above. Identification of upper teeth mesial to P^4 is more indirect. In the case of P^3 this was done by comparison with P^3 of the holotype of *G. latidens*. This cranium also has P^2, but the teeth from Creechbarrow which resemble P^2 are no larger than *G. latidens* P^2 and, in contrast, have a parastyle. Two likely possibilities are that mesial premolars are intra- or inter-specifically variable in size, or that these small P^2-like teeth are P^1s which resemble P^2 in morphology, or both. M37403 is identified as the upper canine by comparison with that tooth of *A. leemanni* (see Hürzeler, 1948*a*: 346, figs 2c, 3b, 4b). A possible upper incisor of *A. leemanni* was figured by Hürzeler (1948*a*: 346, figs 2d, 3c). The tooth which he figured (1948*a*: 351, figs 10c, 11c, 12c) as the lower canine contrasts strongly with the lower canine of *A. eocaenicus* in being less procumbent and having oblique wear extending down one side of the crown like the upper canine. It is also almost identical to the erupting right I^2 of *Pholidocercus* (Koenigswald & Storch 1983: fig. 19). It is tentatively identified as I^2 and Hürzeler's possible upper incisor as I^3. Koenigswald & Storch (1983: 472) identified these teeth as DP_1 and DP^1 respectively in *A. leemanni*. The lingual wear of the former, however, would make it an upper not a lower tooth.

No tooth has been recognized as a potential I^1, but four teeth from Creechbarrow have similar shape and wear to the *A. leemanni* ?I^2. They differ in having a more bulbous lateral outline and a prominent ?metastyle. On one (M36227) a mesial interstitial facet suggests the presence of an I^1. The paracone forms a rib on the lingual wall and the wear facetting extends along this as well as on the ?metastyle and all along the mesial edge of the tooth, which forms a lingually salient ridge from the tip of the paracone to the crown base.

Table 5 Length (l) and mesial (w_1) and distal (w_2) width measurements of teeth of *Gesneropithex figularis* sp. nov. from Creechbarrow. M35420 (*) the holotype; all other specimens paratypes. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M36227	RI^2?	1·95	1·10	
M36226	LI^2?	1·80	1·10	
M36225	RI^2?	2·20	1·10	
M37404	RI^2?	(1·90)	(1·10)	
M37142	RI^3?	1·80	1·05	
M36793	LI^3?	2·00	1·20	
M37403	LC^1	1·75	1·15	
M37141	LP^2?	1·75	0·85	
M36442	LP^2?	1·60	1·00	
M35652	RDP^3?	2·55	–	
M35651	LDP^3?	(2·40)	–	
M37405	RDP^3?	2·50	1·80	
M36417	LP^3	3·05	–	
M37133	LP^4	3·25	–	
M35653	LP^4	3·30	3·70	
M36383	LP^4	–	–	
M35417	LM^1	3·85	(3·75)	
M35654	RM^1	3·90	3·90	
M35419	LM^1	–	4·00	
M37134	LM^1	3·80	–	
M35420*	RM^2	3·80	(4·40)	
M35418	LM^2	3·70	4·25	
M35655	LM^2	3·90	4·50	
M35657	RM^2	–	–	
M37135	LM^2	4·15	4·85	
M37136	RM^2	–	(4·30)	
M35658	LM^3	2·95	3·75	
M35656	LM^3	3·15	3·75	
M35659	LM^3	3·50	4·05	
M35660	LI_1?	–	1·25	
M37138	RI_1?	2·30	–	
M35661	LI_1?	–	1·35	
M37139	LI_1?	2·80	1·20	
M35663	RI_2	2·30	0·90	
M35662	LI_2	2·15	0·90	
M35664	RI_2?	–	1·15	
M35665	LI_3	(2·40)	1·00	
M35667	RI_3	–	(0·95)	
M35666	RI_3	2·60	0·80	
M35668	RC_1	2·55	1·00	
M35670	LP_1	(2·50)	1·10	
M37120	LP_1	2·60	1·30	
M35672	RP_1	2·25	1·10	
M35671	LP_1	2·30	1·05	
M35673	RP_1	2·85	1·00	
M37121	RP_1	2·20	1·00	
M35674	RP_1	–	–	
M35669	LP_1	2·20	1·10	
M35675	RP_1	2·65	1·30	
M35676	RP_2	2·40	1·25	

Table 5 continued

Table 5 Continued

No.	Tooth	l	w_1		w_2
M37123	LP_2	2·65		1·65	
M37122	LP_2	(2·90)		1·65	
M35403	RP_2	2·50		1·45	
M35404	RP_2	2·65		1·55	
M35402	LP_2	2·20		1·30	
M35677	LP_3	2·35		1·35	
M35678	LP_3	2·50		1·50	
M35684	RDP_4	–	1·85		–
M37124	LDP_4	–	1·65		–
M35681	RP_4	3·60		(2·15)	
M35680	LP_4	3·40		(1·85)	
M35679	LP_4	(3·30)		2·05	
M35682	RP_4	(3·70)		2·10	
M35405	RP_4	–		2·05	
M35406	RP_4	3·60		2·05	
M37125	LM_1	(3·75)	(2·85)		3·00
M35685	LM_1	4·00	2·80		(2·95)
M35407	RM_2 in jaw	4·55	3·10		3·40
M35683	RM_2	3·85	2·90		(3·10)
M35409	RM_2	4·40	3·55		3·45
M37126	RM_2	4·05	3·20		3·50
M37129	RM_3	–	–		–
M37128	LM_3	(4·00)	3·00		2·70
M37691	RM_3	–	–		2·55
M37690	LM_3	(3·75)	2·65		2·40
M35688	LM_3	3·85	3·15		2·75
M35689	RM_3	–	–		2·60
M35412	RM_3	–	2·50		2·30
M35410	RM_3	3·75	2·70		2·55
M35411	RM_3	–	–		2·90
M37130	RM_3	4·15	3·20		2·85

?I^3 is intermediate in morphology between I^2 and the upper canine. It has small ?parastyle, the mesial margin being less ridged, and a smaller ?metastyle. The distribution of facetting is similar to that of ?I^2 but less extensive.

The upper canine differs from that of *A. leemanni* in having small ?parastyle and ?metastyle.

$P^{1/2}$ is smaller and lower-crowned than I^3 and has prominent parastyle and metastyle. *G. latidens* P^2 and *A. leemanni* ?P^1 in contrast have no parastyle. There appears to have been a single root pinched in the middle. All the more mesial upper teeth are single-rooted with no sign of pinching, whilst all the more distal upper teeth have three roots.

P^3 has the protocone broken off but this cusp must have been much smaller than on P^4. Length of this tooth, however, is much closer to that of P^4 than it is in *G. latidens* or *G.* aff. *grisollensis*. The morphology is, however, quite similar.

Teeth differing from P^3 only in being smaller and having thinner enamel, a lower paracone, very small metacone on the postparacrista, larger parastyle and metastyle and very small protocone are identified as DP^3.

P^4: on M36383, the rather buccally orientated postprotocrista joins the distal cingulum, as on *G. grisollensis*; on M35653 it stops short and the distal cingulum extends more lingually as in *G. latidens*. There is no sign of a metacone, but a small cuspule occurs in M35653 and M37133 immediately mesial to the metastyle. A similar condition occurs in a P^4 of *G. grisollensis* from Grisolles where there also occurs a second more mesial cuspule which probably represents a metacone.

The morphology of the upper molars is essentially the same as in *G. grisollensis.* There is individual variation in the development of the pre- and post-paraconule cristae: one or other may be missing. There is also some overlap in the morphology of M^2 and M^3. For instance the M^2, M35655, has a distal interstitial facet, but has a relatively lingually tapering outline with smaller hypocone than usual and a large mesostyle like M^3. Conversely, the M^3, M35656, has no distal interstitial facet and is the correct size for M^3 (smaller than M^2), but has only a slightly lingually tapering outline and a large hypocone like M^2. These variations can most simply be explained by differing positions of the field of development of various characters with respect to the tooth (see Butler, 1939, 1967).

?I_1 differs from I_2 in being larger, the crown base being relatively broader, the mesial and distal edges flaring occlusally and the angle of the occlusal with the mesial edge being slightly less acute. The mesial interstitial facet is also longer and extends further down the crown, which on this side passes basally straight into the root without changing orientation. From the preserved I_1 alveoli on the two Hordle Cliff jaws, the tooth was just as procumbent as I_2 (cf. Heller 1935: pl. 1, figs 1a, b) but judged from the mesial interstitial facet must have been orientated more transversely in the jaw. M37139 is unworn and shows a faintly scalloped edge but is not deeply dissected like the lower incisors of the adapisoricid *Litolestes* (see Schwartz & Krishtalka, 1976). From overall size and the size and extent of the bevelled worn edges of M35660 and M35661, I^1 must have been at least as large as ?I^2 and have occluded along the whole length of I_1. Whether or not there was an upper mesial diastema is not certain.

I_2 is much the same as in *A. eocaenicus.* The mesial and distal crown edges are parallel and the mesial one flares slightly mesially away from the root. The mesial interstitial facet is restricted to the occlusal end of the mesial crown margin and is parallel to the mesial edge of the root.

I_3 is blade-like, very procumbent, and mesially evenly tapering; the protoconid shows lingually as a rib but projects little if at all occlusally. The mesial interstitial facet is oblique immediately below the mesial end of the crown.

The lower canine is blade-like and procumbent like I_3 but the mesial taper is less marked and the protoconid projects occlusally. Midway along the distal crest of the protoconid is a concave, buccally bevelled facet caused by contact with the upper canine. The mesial interstitial facet is in the same position as on I_3.

P_1 is less blade-like, has a rounded distolingual shelf, a small talonid cusp and a shorter mesial overhang than in the canine. The mesial interstitial facet is more horizontal and is further under the mesial overhang. M35673 has a more delicate cuspate aspect than the other specimens and might be a deciduous tooth.

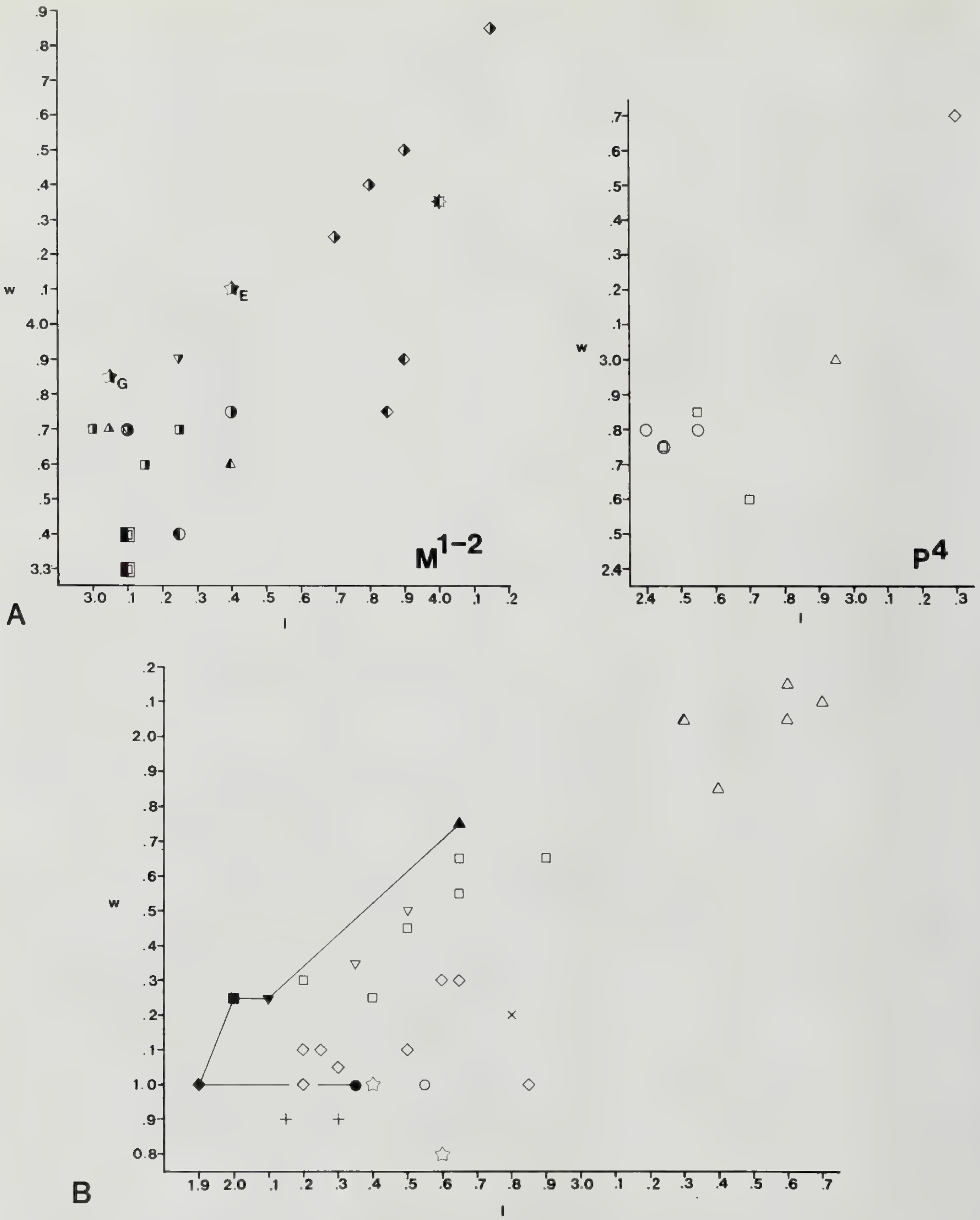
P_2 is less procumbent than P_1, has very weak development of metaconid and protostylid (often situated low down on the distal slope of the protoconid) and the talonid consists of a transverse ridge forming the distal crown margin and rising buccally to form a small ?hypoconid.

P_3 is like P_2 but relatively shorter, more upright, less procumbent, and with a distinct mesially projecting paraconid. It thus contrasts with *A. eocaenicus* in which P_3 is almost identical to P_2. An alternative is that some P_3s have been misidentified as P_2s. From alveolar evidence, this and all the more mesial teeth were single-rooted, those more distal double-rooted.

P_4 is much the same as in *G. grisollensis* but the preprotocristid appears to have a more buccal sweep and the paraconid may be bicuspid.

Two trigonid fragments are identified as DP_4 on the basis of low crown height, thin enamel and mesially projected paraconid region. Protoconid and metaconid are subequal in height. M35684 is unworn and shows a papillate paraconid.

Of the lower preultimate molars, one can be confidently assigned to M_2, as the tip of its broken root was found *in situ* in an otherwise edentulous mandibular fragment (M35407). The tooth has been restored to its original position in the jaw. There is less difference between its mesial and distal width measurements than some isolated teeth which also have a longer trigonid. The latter are here identified as M_1. Overall morphology is almost identical to that of *G. grisollensis* M_1s and M_2s.



Text-figure 14 A, scatter diagrams of length (l) against width (w) in M^{1-2} and P^4 of species of *Gesneropithex*. △ = *G. latidens* (Teilhard); □ = *G. grisollensis* (Louis & Sudre) from Grisolles; ○ = *G.* aff. *grisollensis* from the Hordle Cliff Mammal Bed; ▽ = *G.* aff. *grisollensis* from Hordle Cliff (Rodent Bed?); ◇ = *G. figularis* sp. nov. from Creechbarrow; ☆ = *G. peyeri* Hürzeler from Gösgen Pumpstation (G) and Eclépens B (E); ✲ = *G.* sp. indet. from Robiac. Symbols filled in on left are M^1s, those filled in on right are M^2s. B, scatter diagram of length against width in $I_{1?}$–P_4 of *Gesneropithex figularis* from Creechbarrow (crosses and outline symbols) and C_1–P_4 of *Amphilemur eocaenicus* Heller (syntype GH.7416) from Geiseltal (solid symbols linked by line). × = $I_{1?}$; + = I_2; ☆ = I_3; ○ = C_1; ◇ = P_1; □ = P_2; ▽ = P_3; △ = P_4. Measurements in millimetres.

M_3 shows considerable variation in size and hypoconulid development. The hypoconulid may be nearly as large as the entoconid, situated slightly lingual to the midline and distinctly separated from either entoconid or hypoconid (e.g. M37130) or it may be smaller, lingual in position and completely fused to the entoconid (e.g. M35410). M35688 is intermediate in morphology. Louis & Sudre (1975) described M_3 of *G. grisollensis* from three teeth whose morphology is like M37130.

Relationships. There appear to have been at least four lineages of *Gesneropithex* in total, spanning Auversian to mid-Ludian (viz. *G. peyeri*, *G. grisollensis–latidens*, *G. figularis* and the *G.* sp. from Robiac). They were probably derived from a species of *Amphilemur* of the early to middle Lutetian, but curiously no member of the Amphilemuridae is known from the rich late Lutetian to Auversian Egerkingen fissure deposits. Louis (1976: 49), however, recorded some teeth from the Auversian locality of Arcis-le-Ponsart, which he considered were close to *G. grisollensis*.

Additional records of *G. peyeri*, as used in comparisons in this paper (e.g. Text-fig. 14A) are based on an unworn M^2 (NMB Mt1227) and a DP^4 (NMB Mt1465) from Eclépens B. It is also probable that the M^1 and DP^4 figured by Sudre (1969*a*, 1978*b*) as dichobunid artiodactyls belong to the same species as his *G.* sp. from Robiac (Sudre 1969*b*). The hypocone being larger than the metaconule on both would be unusual for *Mouillacitherium*, as he himself noted (1978*b*), and also for artiodactyls generally. The outline and cusp pattern is typical of *Gesneropithex* and probably represents a new species. An M_2 (CGH RC29) from Robiac is virtually unworn and shows some special features.

G. figularis appears closely related to *G. grisollensis*, which in turn is almost indistinguishable from *G. latidens* in many features. Comparisons are also hampered because the holotype of *G. latidens* is unique and from an unknown stratigraphical level. There is some variation in development of the 'erinaceid' crest in *G. grisollensis* despite Louis & Sudre's (1975) statement. On *G. latidens* there is overall less cresting of the cusps, longer mesial upper molar cingula and more continuous ectocingulum, but it is not clear whether this is merely individual variation. Specimens of *Gesneropithex* from the Mammal Bed and ?Rodent Bed, Hordle Cliff, are difficult to classify, some looking like *G. grisollensis*, others more like *G. latidens*. None have the P^4 distal cingulum bypassing the incipient hypocone and passing lingually, or such a weak distal hypocone crest as in *G. latidens*; in P^4 size the Mammal Bed specimens are more like *G. grisollensis*, but the P_4 metaconid appears to be smaller.

Species of *Gesneropithex* have a patchy stratigraphical and geographical distribution so it is not surprising to find a new species at Creechbarrow. It seems likely that *G. figularis* became extinct before the Ludian, being replaced in southern England by the smaller *G.* aff. *grisollensis*.

Family **NYCTITHERIIDAE** Simpson 1928

The modern concept of this family was first proposed by Robinson (1968). European members were treated in detail by Sigé (1976) who divided the family into two subfamilies: Nyctitheriinae Simpson 1928 and Amphidozotheriinae Sigé 1976. Earlier history of the family was briefly given by Cray (1973: 36) and need not concern us here.

Subfamily **NYCTITHERIINAE** Simpson 1928

Type genus. *Nyctitherium* Marsh 1872.

Included genera. *Leptacodon* Matthew & Granger 1921; *Saturninia* Stehlin 1940; *Scraeva* Cray 1973; and *Pontifactor* West 1974.

Range. Middle Palaeocene to late Eocene, North America; early Eocene to early Oligocene, Europe.

Diagnosis. See Robinson (1968).

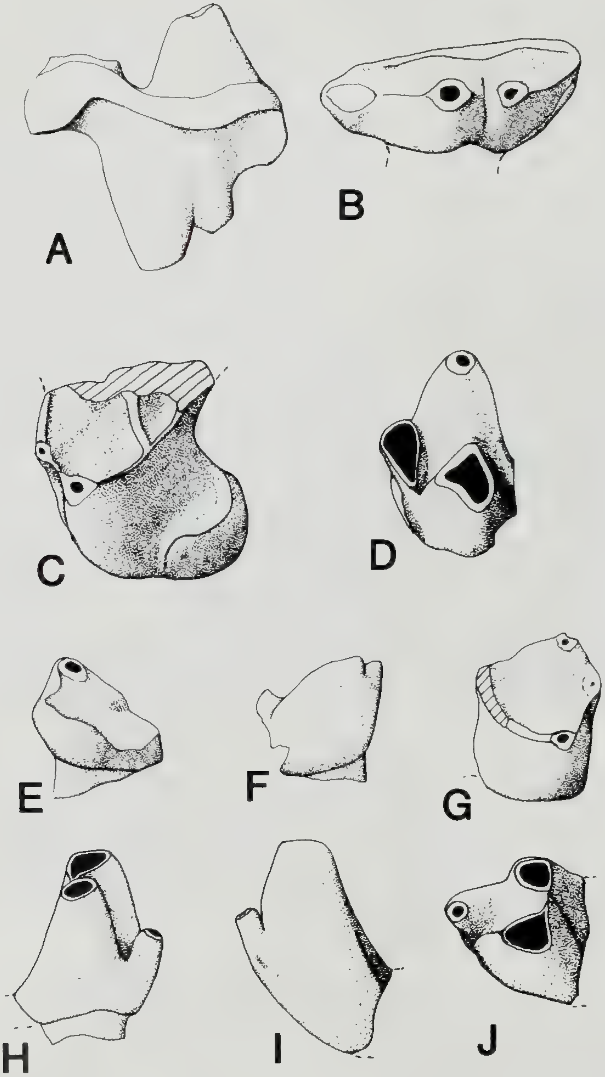
Genus *SCRAEVA* Cray 1973
[= *Arvaldus* Cray 1973]

TYPE SPECIES. *Scraeva hatherwoodensis* Cray 1973. *Microchoerus* Bed, upper Middle or lower Upper Headon Beds; Headon Hill, Isle of Wight.

INCLUDED SPECIES. *S. woodi* Cray 1973.

RANGE. Bartonian (Creechbarrow Limestone) to Ludian (Bembridge Limestone), southern England.

DIAGNOSIS. See Cray (1973: 37) and Sigé (1976: 11, 78).



Text-figure 15 *Scraeva* sp. indet., from Creechbarrow. All × 20. A–B, right P^4 fragment (reversed) (M35647). A is buccal and B occlusal view. C, occlusal view of left $M^{1/2}$ (M35648). D, occluso-buccal view of left lower molar trigonid (M35649). E–G, right $M_{1/2}$ talonid (reversed) (M35424). E is lingual view, F buccal and G occlusal view. H–J, right P_4 trigonid (reversed) (M35650). H is lingual view, I buccal and J occlusal view.

Scraeva sp. indet.
(Text-fig. 15)

v. *1977b* Nyctitheriidae indet.; Hooker: 141.
v *1980* *Scraeva* sp.; Hooker & Insole: 37.

MATERIAL. Right P^4 buccal fragment (M35647); two left $M^{1/2}$ fragments (M35422, M35648); right $M^{1/2}$ fragment (M37143); right P_4 trigonid (M35650); left $M_{1/2}$ talonid (M35423); right $M_{1/2}$ talonid (M35424); left lower molar trigonid (M35649).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. The material representing this taxon is poor, but both $M_{1/2}$ talonid fragments show the presence of a mesoconid, the only character by which this genus can be distinguished from *Saturninia* (see Text-fig. 15E). The size of the specimens appears intermediate between that of *S. hatherwoodensis* and *S. woodi*.

No upper teeth of *Scraeva* have been published, although two upper molars were figured in a thesis by Insole (1972: pl. 6, figs 1–2). The right P^4 fragment from Creechbarrow lacks the protocone. The connate paracone and metacone are tall cusps, the latter shorter and narrower than the former. The parastyle is prominent and the tooth was very waisted between the paracone/metacone region and the (now missing) protocone region. These last two characters are present in Sigé's (1976: 41, fig. 46; 42, fig. 48) figures of P^4s of *Saturninia hartenbergeri* Sigé 1976. In *Saturninia* the P^4s especially are intraspecifically variable for some features (see Sigé 1976: 22, fig. 12), but it is noteworthy that the paracone and metacone are lower and further apart in *Scraeva woodi* and *Saturninia gracilis* than in M35647.

The best preserved of the three $M^{1/2}$s (M35648) is lacking the buccal region along with the parastyle, paracone, metacone and metastyle. The postparaconule crista is weak but the premetaconule crista is strong as in *S. woodi*. The hypocone is prominent and the postflexus is deep as in *S. woodi*. The precingulum is weak like *S. woodi*, not as strong as is usual in *S. hartenbergeri*. The development of the premetaconule crista is like not only *S. woodi* but also *Saturninia grisollensis* Sigé 1976 and *S. hartenbergeri*.

The P_4 trigonid, although slightly worn, appears overall higher than in *S. hatherwoodensis* or *S. woodi*. This would fit with the relatively high paracone and metacone of P^4. The metaconid appears relatively higher than in *S. hatherwoodensis* but this feature seems variable in *S. woodi*.

COMMENTS ON THE STATUS OF *Scraeva*. It is accepted that *Scraeva* and *Saturninia* are very closely related (see Sigé 1976: 78–79), but on the basis of the meagre Creechbarrow material their dichotomy must have been before the Bartonian. Oddly, however, Sigé's (1976: 57, fig. 73) figure of $M_{1/2}$ of *Saturninia grandis* Sigé 1976 shows a mesoconid. Sigé did not mention the character in his description. As *S. grandis* is the largest species of *Saturninia*, approximately equal in size to *Scraeva woodi*, it is worth considering the possibility that the presence of a molar mesoconid is purely a feature of large size, not of generic relationships. This argument is weakened by the fact that another large species of *Saturninia*, *S. beata*, apparently has no mesoconid. It is also possible of course that *Saturninia grandis* should be considered a *Scraeva*. Conclusions of this kind cannot be made on the basis of the poor material from Creechbarrow but must await fuller study of material from the Fluvio-marine series in comparison with *Saturninia* species.

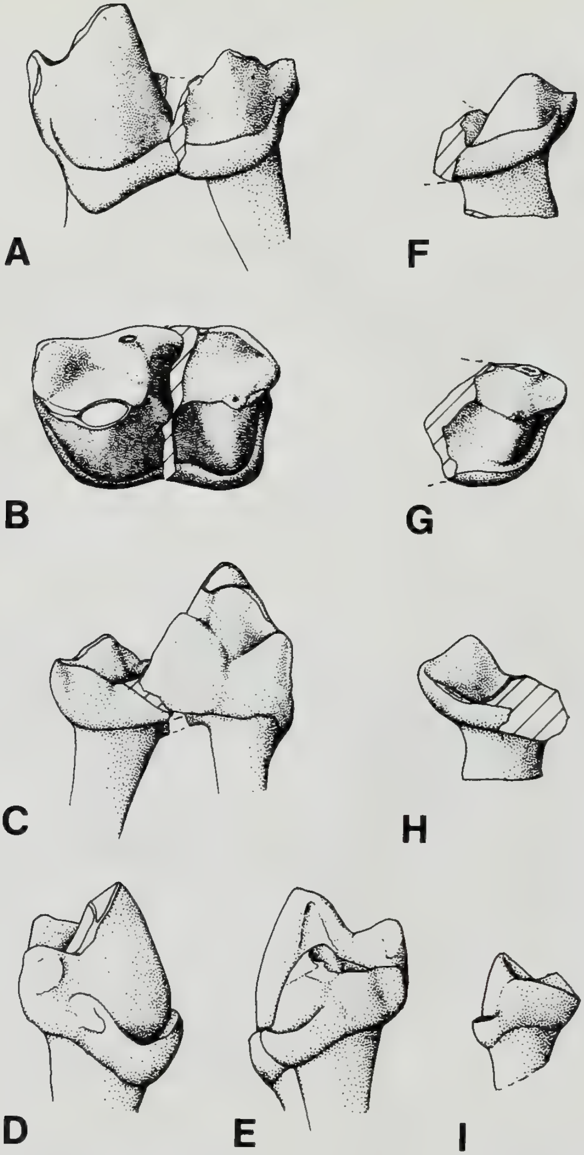
Order **CHIROPTERA** Blumenbach 1779

Suborder **MICROCHIROPTERA** Dobson 1875

Microchiroptera gen. et sp. indet. 1
(Text-fig. 16)

v. *1972* ?Omomyoidea indet.; Hooker: 180–181.
vp. *1980* Chiroptera indet.; Hooker & Insole: 38.

MATERIAL. Left lower molar trigonid fragment (M35710); left $M_{1/2}$ talonid fragment (M35712); right M_3 talonid fragment (M29090).



Text-figure 16 Microchiroptera gen. et sp. indet. 1. A–E, left lower molar trigonid fragment (M35710) and left $M_{1/2}$ talonid fragment (M35712), almost certainly same specimen, from Creechbarrow. Views: A, buccal; B, occlusal; C, lingual; D, mesial; E, distal. F–I, right M_3 talonid fragment (reversed) (M29090) from the Barton Clay (Bed F?), Barton. Views: F, buccal; G, occlusal; H, lingual; I, distal. All × 16·5.

HORIZONS AND LOCALITIES. M29090 is from the Barton Clay (probably around Bed F), Barton Cliff at Barton-on-Sea; the others are from the Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. M35710 and M35712 were found in the same excavation hole. Although they are of identical preservation, size and wear their actual physical fit is poor. Nonetheless this is probably due to abrasion during weathering of the limestone and they almost certainly belong to the same specimen, a left $M_{1/2}$. Its length is estimated 2·00 mm, the trigonid width is 1·22 mm and talonid width 1·25 mm.

It is a robust, fairly low-crowned tooth. It is somewhat worn on the lingual sides of the protoconid and hypoconid tips and the paracristid. There are extensive buccal phase facets on the mesiobuccal walls of the protoconid, precingulid and hypoconid and smaller ones on the distobuccal edges of the protocristid, postmetacristid, postcristid and hypoconulid. The tip of the hypoconid is chipped on the buccal side. There is a continuous buccal cingulum terminating with the precingulid and postcingulid. This parallels the basal crown margin which undulates round the trigonid, reaching a low point at the mesiobuccal corner. There is essentially no ectoflexid. There are abraded patches on the mesial sides of the paraconid and the lingual end of the precingulid, but it is not certain whether or not they represent interstitial facets.

The trigonid is long but the paracristid curves lingually to join the paraconid. The metaconid is a prominent cusp, very slightly higher than the paraconid but much lower than the protoconid. It is strongly salient mesial of the deeply notched protocristid. The protoconid has a prominent lingual rib. The talonid is much lower than the trigonid, and narrower at the cusp tips although the same width basally. The hypoconulid is only slightly nearer the entoconid than the hypoconid, thus not being truly nyctalodont (see Menu & Sigé 1971). An important feature is the very low crestiform entoconid, which is little more than an occlusally convex bulge of the entocristid and lower than the hypoconulid. The cristid obliqua is essentially longitudinal, slightly concave buccally and joins the protoconid just buccal of the trigonid notch.

M29090 is smaller than M35712 (0·93 mm wide) and has no distal interstitial facet. It is slightly narrower and the hypoconulid protrudes further distally. The entoconid is worn but was of similar morphology to M35712, although probably even lower. In other respects the two talonids are almost identical.

The curious character of the entoconid in both suggests that they may belong to the same taxon.

Discussion. The hipposiderid *Palaeophyllophora* Revilliod 1917*b* is similar in having a relatively low semi-nyctalodont talonid with often weak entoconid (see Sigé 1978: pl. 1, fig. 2). However, the entocristid is nevertheless high, the whole tooth is higher-crowned, the talonid is shorter relative to the trigonid, the paracristid is obliquely straight and the cusps are less prominent.

The archaeonycterine palaeochiropterygid *Archaeonycteris* Revilliod 1917*a* has a lower molar trigonid rather similar to the Creechbarrow specimen (see Russell & Sigé 1970: pl. 6, figs 1c, 3). It also has a similarly-placed hypoconulid and can have a fairly weak entoconid (see Russell *et al.* 1973: text-fig. 6i).

Other European Palaeogene bats show little in common with this taxon from Creechbarrow and Barton. The low tubercular nature of the teeth and the near median hypoconulid are primitive characters and suggest affinities with the superfamily Palaeochiropterygoidea Revilliod 1917*a*. The special entoconid character perhaps suggests closer affinities with *Archaeonycteris* than with any other genus, but certain other specializations are probably only convergent with *Palaeophyllophora*. Should it become better known, it may be found to be a new genus.

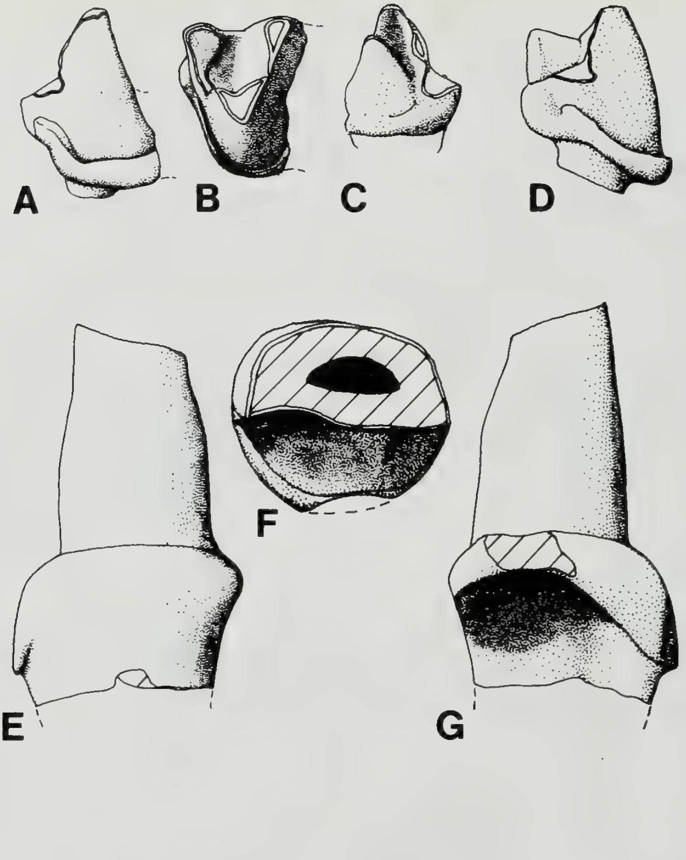
Microchiroptera gen. et sp. indet. 2
(Text-fig. 17A–D)

vp. *1980* Chiroptera indet.; Hooker & Insole: 38.

Material. Left lower molar trigonid (M35711).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. The fragment is 1·17 mm wide. The trigonid is buccally acute with a straight, slightly oblique paracristid. The buccal cingulum is complete to the precingulid. The metaconid



Text-figure 17 Microchiroptera from Creechbarrow. A–D, left lower molar trigonid fragment (M35711) of Gen. et sp. indet. 2. Views: A, buccal; B, occlusal; C, lingual; D, mesial. E–G, left upper canine (M36790) of Gen. et sp. indet. 3. Views: E, buccal; F, occlusal; G, lingual. H–J, left lower canine (M36421) of Gen. et sp. indet. 4. Views: H, buccal; I, occlusal; J, lingual. All × 16·5.

is slightly salient mesially. The protoconid is concave lingually. The paraconid is heavily worn and would probably have been slightly lower than the metaconid. The edges of the paracristid and protocristid and the tips of the protoconid and metaconid are slightly worn. The tooth as a whole is slightly corroded.

Discussion. The fragment is more gracile, more crestiform and has higher cusps than M35710, which also differs in many of the characters described. It must therefore represent a different taxon from Microchiroptera gen. et sp. indet. 1. Unfortunately the talonid is missing and the morphology of the trigonid could be encountered in a very wide variety of microchiropteran taxa.

Microchiroptera gen. et sp. indet. 3

(Text-fig. 17E–G)

Material. Left upper canine (M36790).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. Much of the main cusp is broken away and parts of the lingual cingulum are abraded. In occlusal view the tooth is subovoid in outline. The strong shelf-like lingual cingulum continues round the mesial edge where it migrates further up the crown. Distobuccally there is a slight ridge-like basal swelling not developed into a true cingulum. The lingual side of the main cusp is concave, the buccal side convex. Length is 1·77 mm, width 1·53 mm.

Discussion. What is preserved of this tooth is very like the hipposiderid *Pseudorhinolophus* Schlosser 1887, especially in the lingual concavity. A slight difference is that the lingual cingulum is slightly shallower at its distal end. Size is similar to that of *P. weithoferi* Revilliod 1917*b*. If the similarities indicate true affinities with this genus, M36790 cannot belong to Microchiroptera gen. et sp. indet. 1. Although Microchiroptera gen. et sp. indet. 2, amongst many other taxa, could fit in the genus *Pseudorhinolophus*, it is a little small for this upper canine, M36790, to be associated with it.

Microchiroptera gen. et sp. indet. 4

(Text-fig. 17H–J)

Material. Left lower canine (M36421).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. Most of the main cusp is broken away leaving only the distal and lingual areas of the base of the crown together with the root. There is a strong cingulum continuous round the region preserved. The latter is slightly cuspate distally and there are two worn papillae lingually. The main cusp has a prominent lingual rib and a distolingual crest.

Discussion. The mesiolingual angle is more acute than it is in *Pseudorhinolophus* and the lingual cingulum is stronger, so it is unlikely that this tooth belongs to the same taxon as Microchiroptera gen. et sp. indet. 3, but on grounds of size it could belong to either of the other two. It is too incomplete for further comment.

Order **PRIMATES** Linnaeus 1758

Suborder **PROSIMII** Illiger 1811

Infraorder **TARSIIFORMES** Gregory 1915

Family **OMOMYIDAE** Trouessart 1879 (*sensu* Szalay 1976)

Subfamily **MICROCHOERINAE** Lydekker 1887 (*sensu* Simons 1961)

(including Necrolemurinae Simpson 1940 and Pseudolorisinae Simpson 1940)

Type genus. *Microchoerus* Wood 1844.

Included genera. *Pseudoloris* Stehlin 1916, *Nannopithex* Stehlin 1916, *Necrolemur* Filhol 1873 and ?*Pivetonia* Crusafont-Pairo 1967.

RANGE. Late Ypresian to late Ludian, Europe.

INTRODUCTION. I follow Szalay (1976; see especially pp. 168–170 for historical review) in allocating this subfamily to the Omomyidae, rather than Russell *et al.* (1967), who placed it in the Tarsiidae. This is done on grounds of greater morphological similarity. Classically separated from the North American Omomyidae essentially on geographical grounds, the Microchoerinae appear not to have been diagnosed since they have acquired the present generic content, nor since being placed in the present family. It is almost certainly a natural group, as Simons (1961) thought. Szalay (1976: 413) considered that the only features of the Microchoerinae which might separate them from the other omomyids was tibiofibular fusion and extreme inflation of the mastoid, and that the enlarged first lower incisor was a primitive

Table 6 Coefficients of variation for length and width of teeth of Recent *Tarsius*.

		T. bancanus borneanus		*T.b.b. + T. syrichta*		*T.b.b. + T.b. natunensis*		*T.b.b. + T.b.n. + T. syrichta*	
Tooth		N	v	N	v	N	v	N	v
I^1	l	8	4·45	10	8·41	9	4·63	11	8·04
	w	8	9·54	10	10·78	9	9·59	11	10·50
I^2	l	7	4·35	8	4·65	8	5·63	9	5·57
	w	7	4·47	8	10·02	8	4·17	9	9·37
C^1	l	8	4·33	10	5·37	9	5·49	11	5·87
	w	8	4·94	10	9·97	9	4·83	11	9·46
P^2	l	7	4·73	10	7·44	8	7·14	11	8·06
	w	7	3·00	10	11·02	8	3·97	11	10·49
P^3	l	8	7·94	10	7·69	9	7·81	11	7·55
	w	8	3·46	10	3·15	9	3·24	11	3·00
P^4	l	8	5·63	10	5·19	9	6·17	11	5·65
	w	8	5·43	10	5·29	9	5·36	11	5·28
M^1	l	8	3·68	10	3·50	9	3·69	11	3·54
	w	8	2·39	10	3·53	9	2·58	11	3·61
M^2	l	7	2·94	9	2·95	8	3·06	10	3·07
	w	7	2·29	9	2·86	8	2·12	10	2·70
M^3	l	8	4·50	10	4·08	9	4·21	11	3·87
	w	8	5·87	10	5·32	9	5·59	11	5·12
I_1	l	7	3·92	8	4·11	8	4·11	9	4·17
	w	7	7·97	8	7·67	8	8·62	9	8·44
C_1	l	7	5·30	8	5·67	8	6·22	9	6·26
	w	7	7·16	8	7·19	8	6·87	9	6·87
P_2	l	7	6·69	9	6·52	8	7·64	10	7·15
	w	7	3·61	9	9·37	8	5·63	10	9·33
P_3	l	7	5·47	8	5·97	8	5·49	9	5·83
	w	7	5·63	8	6·14	8	5·21	9	5·75
P_4	l	8	8·08	9	7·80	9	9·11	10	8·70
	w	8	6·63	9	6·20	9	7·02	10	6·63
M_1	l	8	5·60	10	4·99	9	5·30	11	4·82
	w	8	3·14	10	3·75	9	4·97	11	4·93
M_2	l	7	6·09	9	5·43	8	5·78	10	5·30
	w	7	3·82	9	3·51	8	5·34	10	4·80
M_3	l	8	3·74	10	3·60	9	4·27	11	4·11
	w	8	4·26	9	4·05	9	5·40	10	5·10

feature of the subfamily. Szalay & Delson (1979: 258) considered the conformation of the enlarged upper and lower first incisors as the primary diagnostic feature. Slight separation of the first pair of upper incisors was considered to differentiate them from the Tarsiidae and other omomyids where the anterior dentition was known. Most of these features are omitted from the diagnosis below as they are known for so few of the genera in the whole family that their value cannot be reasonably assessed.

DENTAL FORMULA. This was interpreted by Simons (1961) as $\frac{2}{0/1}\,\frac{1}{1}\,\frac{3}{4}\,\frac{3}{3}$. Small perforations in the lower jaw anterior to the enlarged lower tooth were thought by him to be the alveoli of a very small incisor. These were reinterpreted by Gingerich (1975*a*, 1976*b*) and Szalay (1975, 1976) as anterior mental foramina. Gingerich (1976*b*: 91) reinterpreted the lower formula as 1 1 3 3 by direct comparison with *Tarsius*. Szalay (1976) in contrast interpreted it as 2 1 2 3 by direct comparison with *Omomys* or *Tetonius* (presumably with respect to their mode of tooth reduction rather than their actual dental formula). If one considers details of occlusion in *Microchoerus* (see Simons 1961: text-fig. 2) it is more reasonable that P^2 should occlude with an equal-sized P_2 rather than with the lower canine as it would have to according to Szalay's interpretation. The small tooth immediately distal to the enlarged lower incisor could then be either the lower canine or I_2. As the larger of the two alternatives in the upper jaw is the canine, it is almost certain that this is the one which would be retained. Thus Gingerich's interpretation of the dental formula is followed here. Consequently it seems that reduction and loss for face shortening has involved teeth different in the Microchoerinae from the Omomyinae or Anaptomorphinae.

EMENDED DIAGNOSIS. Dental formula: $\frac{2}{1}\,\frac{1}{1}\,\frac{3}{3}\,\frac{3}{3}$. $I\frac{1}{1}$ enlarged; upper canine and P^2 subequal, not greatly reduced, approximately same length as P^3; P_{2-3} subequal, slightly smaller than P_4; I^2 and lower canine greatly reduced.

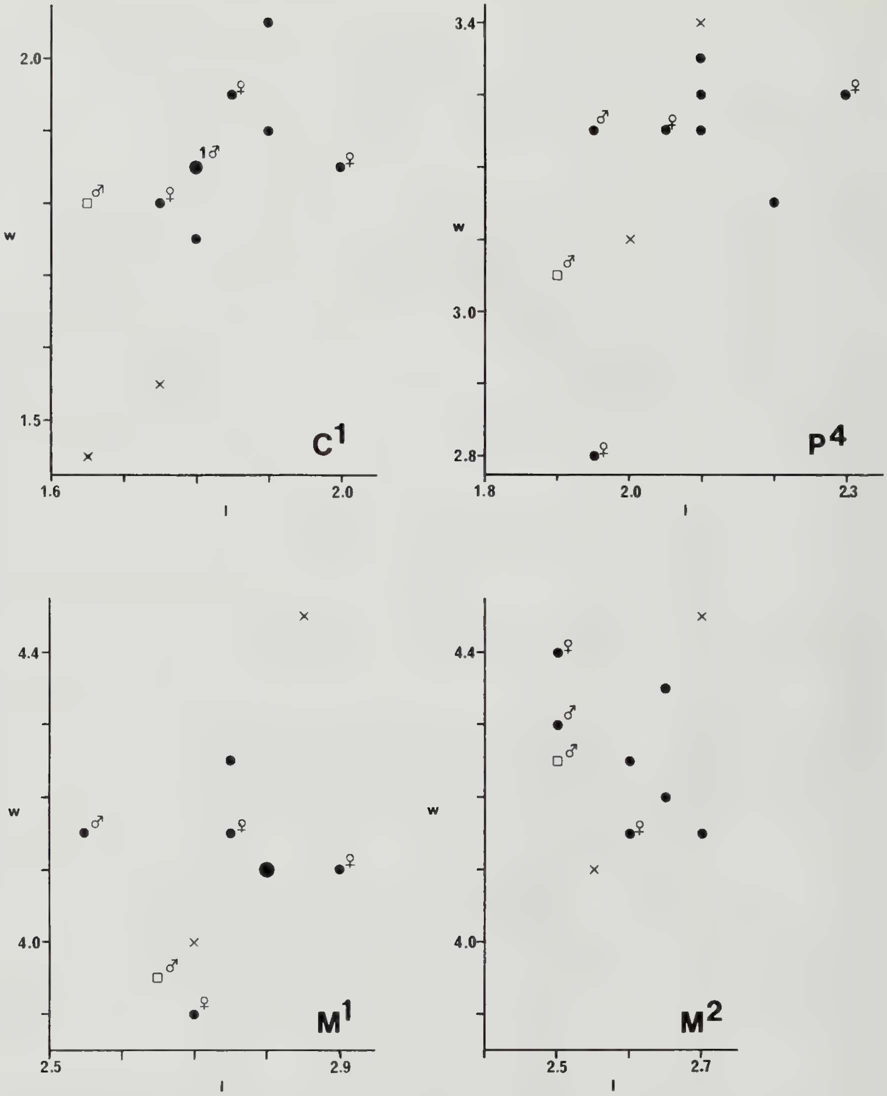
ORIGINS. It is unlikely that the subfamily is derived from *Teilhardina* as Hürzeler (1948*b*) thought, because *Nannopithex* occurs by the late Ypresian (see Hooker & Insole 1980: 38) with already too great modification of the anterior dentition (i.e. enlargement of $I\frac{1}{1}$). As yet fragmentary omomyid remains from the English early Eocene (Hooker 1980, Hooker & Insole 1980) might provide alternative candidates.

RECENT COMPARATIVE MATERIAL. Because of small sample sizes of this subfamily in the Creechbarrow assemblages, and because ranges of variation in some published measurements of *Microchoerus* species are large, I sought an independent control. In searching the literature for tooth measurements of the Recent tarsiid *Tarsius*, I found that Swindler (1976: 68, 210–211, tabs 43–46) gave statistics for length and width of $C\frac{1}{1}$–$M\frac{3}{3}$. Unfortunately Swindler pooled the different species to increase the number of measurements. I have calculated the coefficients of variation of these measurements and the majority are indeed higher than normally found in a single species (see Gingerich 1974). The numbers of specimens available to Swindler were: *T. spectrum* (1 male, 5 females), *T. bancanus* (1 male, 1 female), *T. syrichta* (7 males, 9 females).

I therefore measured the length and width dimensions of all the teeth of Recent *Tarsius bancanus* and *T. syrichta* available in the BM(NH) Zoology Department (a maximum of 12 specimens). The coefficients of variation are given in Table 6, and plots of certain teeth in scatter diagrams in Text-fig. 18. Gingerich (1974: 896) demonstrated that low coefficients of variation (v) were characteristic for cheek teeth of a range of mammalian taxa, mainly primate (from various sources). This did not include *Tarsius*.

Tarsius, as far as the relatively small sample of mainly one species can show, has generally low coefficients of variation for all the teeth. Intraspecific variation is high only in I^1 width, P^3 length, I_1 width, lower canine width and P_4 length. M_1 and M_2 length is more variable than in the corresponding upper teeth and may result partly in variation in size and position of the paraconid and also in its wear. P_4 length variation may be artificially high because it is difficult to measure, being oblique in side view.

The largest sample was of *T. bancanus borneanus* from Borneo. Numbers of other species or subspecies were too low to be compared for v, other than by adding to the data for *T. bancanus*



Text-figure 18 Scatter diagrams of length (l) against width (w) in upper canine, P^4, M^1 and M^2 of species of Recent *Tarsius*; × = *T. syrichta* (Linné) from the Philippines; ● = *T. bancanus borneanus* Elliott from Borneo; □ = *T. bancanus natunensis* Chasen (type) from the S. Natuna Islands. Individuals of known sex are indicated. An enlarged solid circle indicates two identical measurements. Measurements in millimetres.

borneanus to see whether this was then increased or decreased. Either or both happened with the more anterior teeth, but the molars were much more constant (see Table 6). For application of these data to the Creechbarrow microchoerines, see under the relevant species.

Niemitz (1977) made a biometrical study of Recent *Tarsius* and reduced the recognizable species to three, and subspecies to two of *T. spectrum*, possibly two of *T. bancanus* and one of *T. syrichta*. He did not measure the teeth but, comprehensively done, this would seem a worthwhile project. Although the populations of *Tarsius* on the various Far Eastern islands cannot have been separated for long geologically, it is evident that isolation has produced slightly different dimensions for some of the teeth, mainly the unicuspid anterior ones.

Note on measurements. Because of the problem in deciding on the mesiodistal and buccolingual parameters in I^{1}_{1}, the length and width dimensions given for these teeth alone (including Recent *Tarsius*) are anteroposterior and mediolateral respectively.

Genus *NANNOPITHEX* Stehlin 1916

Type species. *Nannopithex pollicaris* Stehlin 1916. Late Lutetian fissure fillings; Egerkingen, Grey Marl Facies (= Huppersand), Switzerland [= *Necrolemur filholi* Chantre & Gaillard 1897, Auversian fissure filling; Lissieu, France (*fide* Simons 1961: 66–67)].

Included species. *N. raabi* (Heller 1930) Simons 1961, *N. quaylei* sp. nov. and *N.* sp. 1. Szalay (1971*a*: 2) synonymized *Pivetonia* Crusafont-Pairo 1967 with *Pseudoloris*. From Crusafont-Pairo's figures, the M_{1-2} paraconids and long trigonids are more suggestive of *Nannopithex*, although size is close to *Pseudoloris parvulus*. Whatever the correct genus, *Pivetonia isabenae* Crusafont-Pairo 1967 is a valid species.

Range. Late Ypresian to Bartonian (Marinesian), England, France, East Germany and Switzerland.

Emended diagnosis. Tooth enamel wrinkling may be present; mesiolingual crest from paracone on I^2–P^4 absent; P^{3-4} paracone–protocone crest present: P^4 metastylar wing short; upper molar *Nannopithex* fold present; M^{1-2} outline subtriangular to subquadrate, broader than long; M^{1-2} hypocone usually much smaller than protocone; M^{1-2} paracone single and metaconule small and usually single; M^{1-2} mesostyle absent; I_2 narrow with distolingual cingulum strong; P_{2-3} relatively moderately elongated with high distal cingula; M_1 trigonid length $\geqslant$ talonid; M_{1-2} protocristid straight and complete; M_{1-2} entoconid lower than metaconid; M_{1-2} hypoconulid very small and single to absent; M_3 hypoconulid lobe moderately broad, short to long, unicuspid to bicuspid; paraconid present on M_{1-2}, usually fusing with metaconid on M_3; angular process may not be expanded; coronoid process may be high.

Nannopithex quaylei sp. nov.

(Pl. 4, figs 9–14; Pl. 5, figs 1, 5; Pl. 6, fig. 1; Text-figs 19–21)

v *1977b* ?*Pronycticebus* sp.; Hooker: 141.
v *1980* *Pseudoloris* sp. 1; Hooker & Insole: 39.

Name. After Mr W. J. Quayle, for help with field work.

Holotype. Left M^2, M37145. Pl. 4, fig. 10.

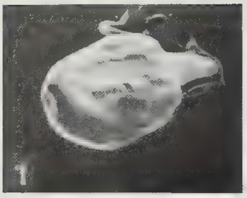
Paratypes (11). Left I^1 (M37154); right I^1 (M35434); left P^4 (M35759); two right P^4s, one almost complete (M35760), the other a buccal fragment (M37144); left M^3 lacking metaconal region (M35721); left I_1 (M35736); left P_3 (M35748); left $M_{1/2}$ talonid fragment (M35720); right $M_{1/2}$ talonid fragment (M35425); left M_3 talonid fragment (M37147).

Doubtful material. Four upper molar fragments (M35426, M35723, M36440, M37146); left M_3 trigonid fragment (M37152).

Horizon and locality.

Diagnosis. Large *Nannopithex*, M^2 length 2·75 mm; tooth enamel surface smooth; P^4 parastyle distinct; M_3 with indistinct entoconid.

Differential diagnosis. *N. raabi*, *N. filholi* and *N.* sp. 1 (p. 251) are smaller, have a distinct M_3 entoconid, the enamel wrinkled in varying degrees and an indistinct P^4 parastyle; *N. raabi* and *N. filholi* appear slightly higher-crowned; *N. filholi* sometimes has a larger M^{1-2} hypocone, broader bicuspid M_3 talonid and higher M_{1-2} entoconid.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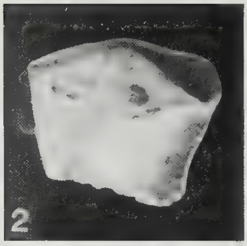
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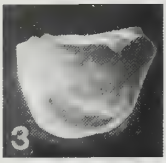
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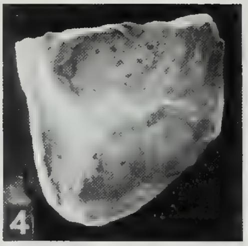
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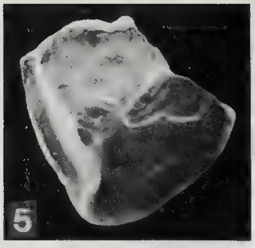
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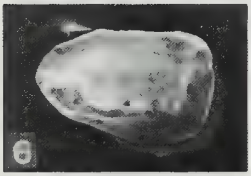
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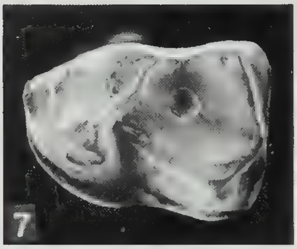
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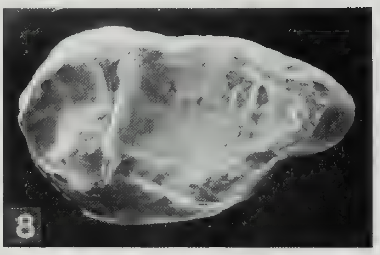
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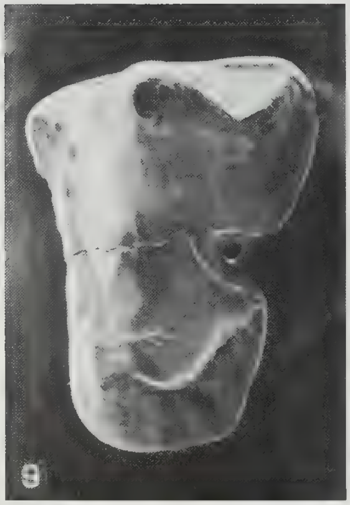
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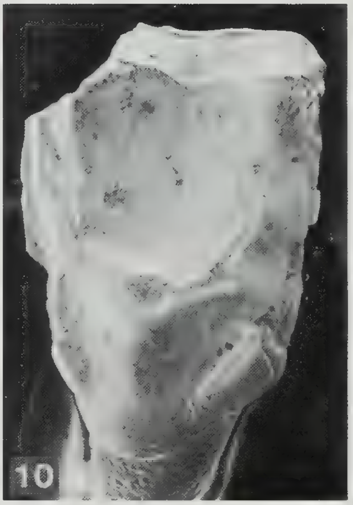
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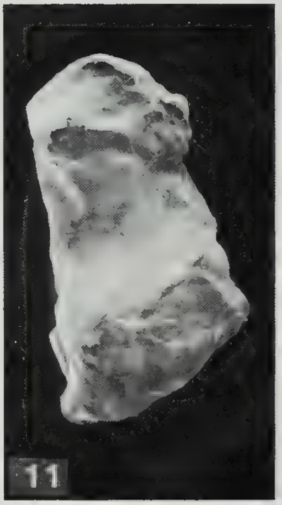
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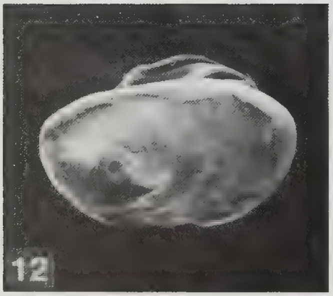
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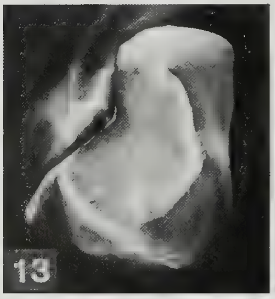
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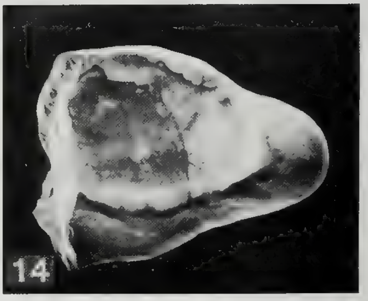

14

Description. Fragmentary representatives of several different important tooth types can be referred to this species. M$\frac{3}{3}$s are not much larger than those attributed to *N.* sp. 1 (q.v.). The characters of the left M_3 talonid used in the diagnosis might be due partly to individual variation. More material is obviously needed (see Text-figs 19–21 for evidence of size separation from *N.* sp. 1).

Even though most of the teeth are slightly worn, this is not thought to have been the cause of lack of enamel wrinkling. The teeth of *N.* sp. 1 in the same states of wear still have visible wrinkling. The $M_{1/2}$ talonid fragments appear longer for their width than in the other *Nannopithex* species but trigonids are unknown.

Most of the other details of the teeth are typical of other *Nannopithex* species and evident from the figures (Pl. 4, figs 9–14, Pl. 5, figs 1, 5 and Pl. 6, fig. 1).

Conclusions. For the first time two contemporaneous species of *Nannopithex* at a single locality are demonstrated, as well as an upward extension of the range of the genus.

Nannopithex sp. 1
(Pl. 4, figs 1–8; Pl. 5, fig. 4; Text-figs 19–21)

v. *1977b* *Nannopithex filholi* (Chantre & Gaillard); Hooker: 141.
v. *1980* *Nannopithex filholi* (Chantre & Gaillard); Hooker & Insole: 38.

Material. Left I^1 (M35728); right I^1 (M35740); left I^2 (M35741); right P^3 buccal half (M37151); right $P^{3/4}$ protoconal fragment (M37161); left M^2 broken buccally (M35724); right $M^{1/2}$ paraconal fragment (M35725); left M^3 protoconal fragment (M35722); left P_2 (M37149); two right M_1s (M35715–6); right $M_{1/2}$ talonid fragment (M35717); two left M_3s (M35427, M37153); right M_3 talonid fragment (M35727).

Horizon and locality.

Description. Much of the material from Creechbarrow is fragmentary, which makes accurate measurement difficult. The typically least variable teeth, the first and second molars, are especially incomplete whereas two M_3s are nearly complete.

Most of the specimens compare quite well with *N. filholi* (including *N. pollicaris*) but are larger. The enamel wrinkling is variable. The M^3 (M35722) is quite large and closer to *N. quaylei* in size than to any other described *Nannopithex* M^3s; it is tentatively distinguished on the enamel wrinkling. Two of the three M_3s (M35427, M37153) are similarly large but have wrinkled enamel in the talonid basin and a prominent entoconid. A tentative conclusion from this evidence is that *N.* sp. 1 has proportionately larger M$\frac{3}{3}$s than *N. filholi*. An alternative explanation is that these teeth belong to *N. quaylei*. However, M35727 is rather smaller than the other two and more material is needed to be certain of this difference.

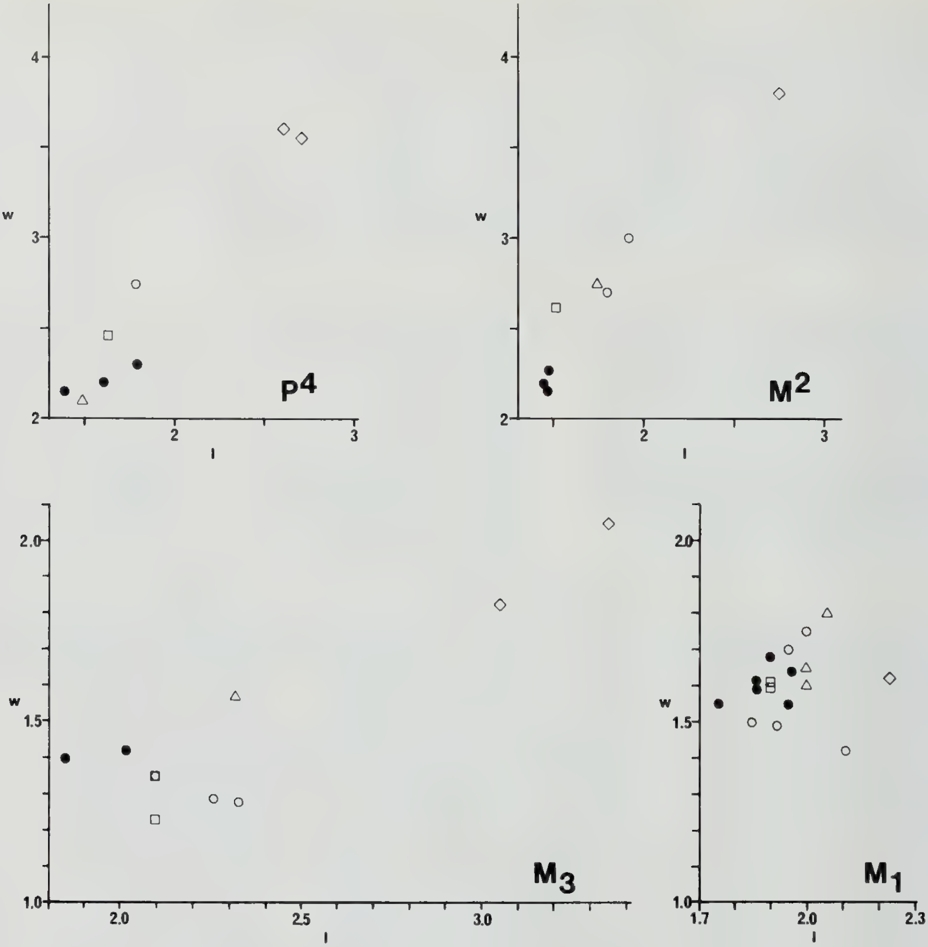
The M_1s (M35715–6) show, better than *N. quaylei*, the *Pseudoloris*-like elongation of the talonid (see Table 9). In this character and in slightly lower crown height they differ from *N. raabi* and *N. filholi*. A fairly close relationship to *Pseudoloris* may be indicated (see Text-fig. 24).

Text-figs 20–21 demonstrate the existence of size variation greater than expected for a single species of *Nannopithex* at Creechbarrow, but the fragmentary nature of some crucial tooth types renders *N.* sp. 1 unnameable in the present state of knowledge.

Plate 4 Scanning electron micrographs of occlusal views of teeth of *Nannopithex* from Creechbarrow, ×15.

Figs 1–8 *Nannopithex* sp. 1. Fig. 1, left I^2 (M35741). Fig. 2, buccal half of right P^3 (reversed) (M37151). Fig. 3, lingual half of right $P^{3/4}$ (reversed) (M37161). Fig. 4, lingual half of left M^2 (M35724). Fig. 5, lingual half of left M^3 (M35722). Fig. 6, left P_2 (M37149). Fig. 7, right M_1 (reversed) (M35715). Fig. 8, left M_3 (M35427). See above.

Figs 9–14 *Nannopithex quaylei* sp. nov. Fig. 9, right P^4 (reversed) (M35760). Fig. 10, **holotype** left M^2 (M37145). Fig. 11, left M^3 lacking metaconal region (M35721). Fig. 12, left P_3 (M35748). Fig. 13, right $M_{1/2}$ talonid fragment (reversed) (M35425). Fig. 14, left M_3 talonid fragment (M37147). See p. 249.



Text-figure 19 Scatter diagrams of length (l) against width (w) in P^4, M^2, M_3 and M_1 of species of *Nannopithex* from various European localities: ○ = Geiseltal (*N. raabi* (Heller)); □ = Bouxwiller (*N. raabi*); ● = Egerkingen γ and Grey Marl Facies (= Huppersand) (*N. filholi* (Chantre & Gaillard)); △ = Lissieu (*N. filholi*); ◇ = Creechbarrow. Data for Egerkingen and Lissieu mainly from Hürzeler (1948*b*). The Creechbarrow plots represent *N. quaylei* sp. nov. for the upper teeth and *N.* sp. 1 for the lowers. Measurements in millimetres.

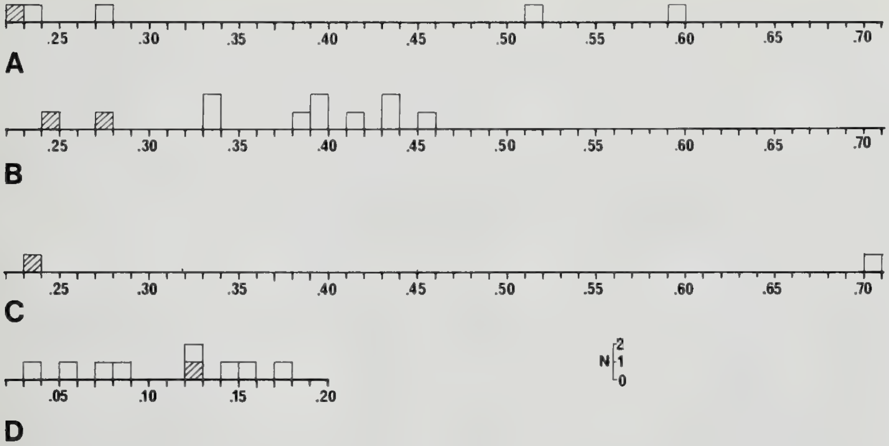
Genus ***PSEUDOLORIS*** Stehlin 1916

TYPE SPECIES. *Necrolemur parvulus* Filhol 1890*b*, from the Phosphorites du Quercy.

INCLUDED SPECIES. *P. reguanti* Crusafont-Pairo 1967 and *P. crusafonti* Louis & Sudre 1975.

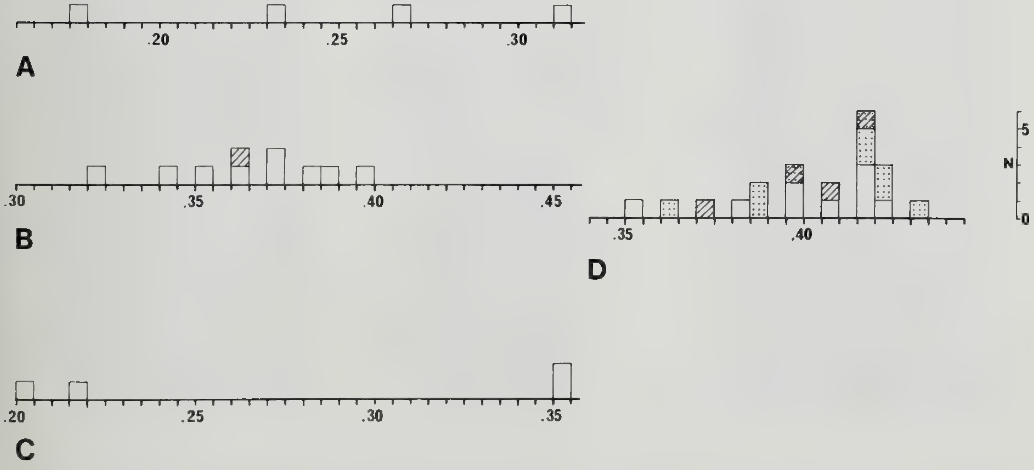
RANGE. Bartonian (Marinesian) to Ludian, England, France, Switzerland, West Germany and Spain.

EMENDED DIAGNOSIS. Tooth enamel wrinkling absent; mesiolingual crest from paracone on I^1–P^4 absent; P^{3-4} paracone–protocone crest absent; P^4 metastylar wing long; upper molar *Nannopithex* fold absent; M^{1-2} outline subtriangular, broader than long; M^{1-2} hypocone



Text-figure 20 Histograms of log. length × width of: A, I^1 of *Nannopithex*; B, I^1 of Recent *Tarsius*; C, I_1 of *Nannopithex*; D, I_1 of Recent *Tarsius*. In A and C, hollow squares = *N. quaylei* sp. nov. and *N.* sp. 1 from Creechbarrow; hatched squares = *N. raabi* (Heller) from Geiseltal. In B and D, hollow squares = *T. bancanus* Horsfield; hatched squares = *T. syrichta* (Linné). Measurements in millimetres.

much smaller than protocone; M^{1-2} paraconule and metaconule small and single; M^{1-2} mesostyle absent; I_1 narrow with distolingual cingulum weak; P_{2-3} relatively very elongated with low distal cingula; M_1 trigonid length equal to talonid; M_{1-2} protocristid straight and complete; M_{1-2} entoconid same height as metaconid; M_{1-2} hypoconulid very small and single to absent; M_3 hypoconulid lobe narrow, short, unicuspid; lower molar paracristid without paraconid on M_{1-3} and not joined to metaconid by crest; angular process not expanded; coronoid process low.



Text-figure 21 Histograms of: A, log. talonid width of M_3 of *Nannopithex quaylei* sp. nov. and *N.* sp. 1 from Creechbarrow; B, log. maximum width of M_3 of Recent *Tarsius*, hollow = *T. bancanus* Horsfield, hatched = *T. syrichta* (Linné); C, log. talonid width of $M_{1/2}$ of *N. quaylei* and *N.* sp. 1 from Creechbarrow; D, log. talonid width of Recent *Tarsius*, hollow = *T. bancanus*, hatched = *T. syrichta*, dotted = M_2, undotted = M_1. Measurements in millimetres.

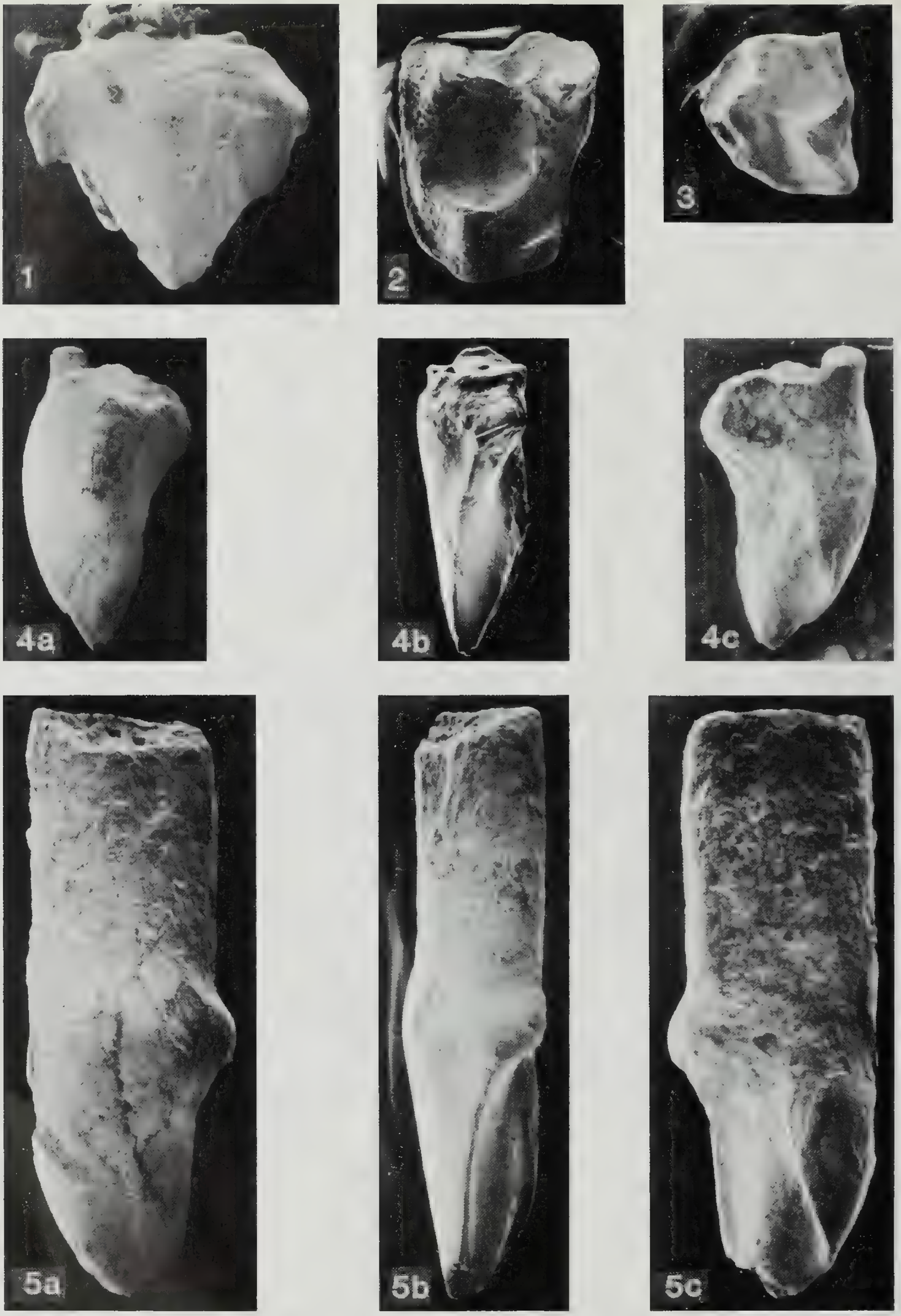


Plate 5 Scanning electron micrographs of teeth of *Nannopithex* and *Pseudoloris* from Creechbarrow, × 15.

Figs 1, 5 *Nannopithex quaylei* sp. nov. Fig. 1, buccal view of right P^4 (reversed) (M35760). Fig. 5a–c, right I^1 (reversed) (M35434); a, lateral (distobuccal), b, posterior (distolingual) and c, mesial views. See p. 249.

Figs 2–3 *Pseudoloris* cf. *crusafonti* Louis & Sudre. Fig. 2, occlusal view of right M^2 (reversed) (M37148). Fig. 3, occlusal view of right M$_2$ (reversed) (M35726), broken distally. See p. 256.

Fig. 4a–c *Nannopithex* sp. 1. Left I^1 (M35728); views as Fig. 5a–c. See p. 251.

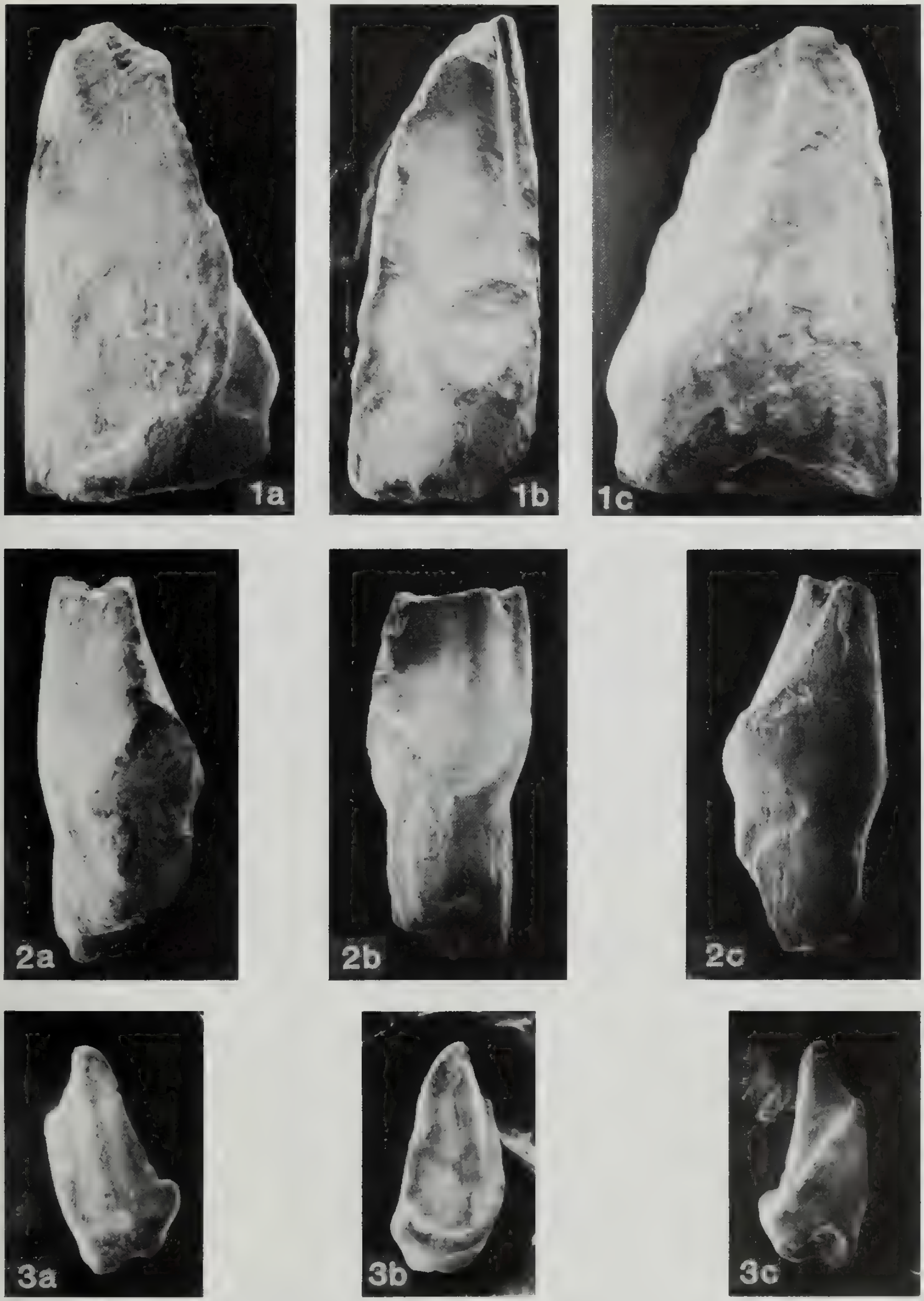


Plate 6 Scanning electron micrographs of lower incisors of *Nannopithex* and *Microchoerus* from Creechbarrow, × 15. Views as Pl. 5, fig. 5a–c.

Fig. 1a–c *Nannopithex quaylei* sp. nov. Left I_1 (M35736). See p. 249.

Figs 2–3 *Microchoerus wardi* sp. nov. Fig. 2a–c, left I_1 (M35747). Fig. 3a–c, left DI_1? (M35719). See p. 259.

Pseudoloris cf. ***crusafonti*** Louis & Sudre 1975
(Pl. 5, figs 2–3; Text-fig. 22)

v. *1977b* *Pseudoloris* cf. *crusafonti* Louis & Sudre; Hooker: 141.
v. *1980* *Pseudoloris crusafonti* Louis & Sudre; Hooker & Insole: 39.

HOLOTYPE OF SPECIES. M^2 (UM GRI.443). Calcaire de St Ouen (Bartonian); Grisolles, Aisne, France.

DIAGNOSIS OF SPECIES. See Louis & Sudre (1975).

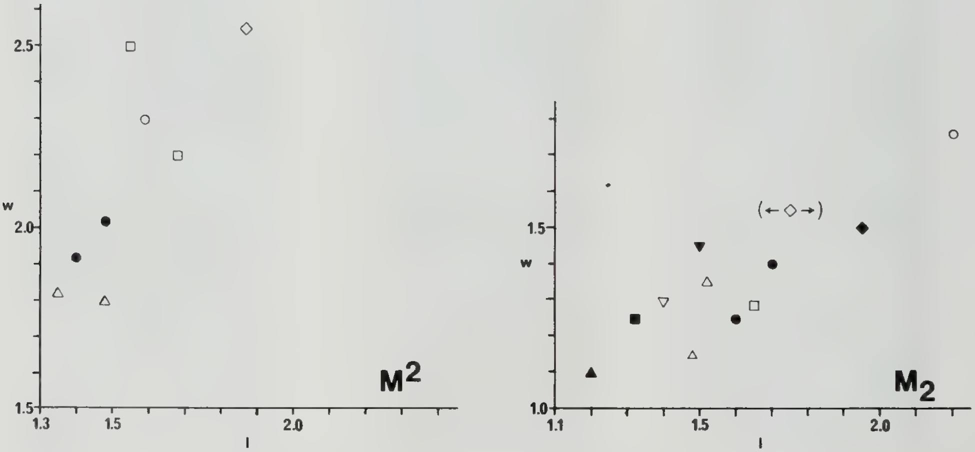
MATERIAL. Right M^2 (M37148) and right M_2 broken distally (M35726).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. *P. crusafonti* was considered by Louis & Sudre (1975) to be intermediate in size between *P. parvulus* and *P. reguanti*. Identification of the Creechbarrow material is complicated by Schmidt-Kittler's (1977*a*: 190–192, text-fig. 11) recent finds in the Ludian fissure filling of Weissenburg 8, southern Germany. On the basis of size, Schmidt-Kittler considered that two species were represented within the *P. crusafonti* assemblage from Grisolles, the lower molars overlapping with *P. parvulus*, the upper teeth being larger. Text-fig. 22 uses Schmidt-Kittler's (1977*a*: text-fig. 11) and Louis & Sudre's (1975: 824, tab. 7) data and adds new material from Creechbarrow and the Hordle Cliff Mammal Bed (the latter mainly in R. Gardner's private collection).

M37148 is slightly larger than either of the Grisolles M^2s or that from Weissenburg 8. It resembles *P. crusafonti* in morphology except for the absence of pre- and post-metaconule cristae. At first sight this seems a relatively insignificant difference, but in all the upper molars of *P. parvulus* available from the Hordle Cliff Mammal Bed, presence of such cristae is constant.

Oddly, M35726 plots close to *P. reguanti* for size, the Weissenburg 8 tooth being larger and the *P. crusafonti* M_2 being smaller. From the pattern encountered in Recent *Tarsius* (p. 247) and Eocene *Microchoerus* (p. 260), $M_{1\ 2}$ are more variable than M^{1-2} in size. Thus it need not be doubted that the type *P. crusafonti* assemblage is homogeneous. More material is needed from all localities for numerical and morphological variation to be evaluated, before definite identification of non-type material can be made.



Text-figure 22 Scatter diagrams of length (l) against width (w) in M_2 and M^2 of species of *Pseudoloris* from various European localities: ● = Hordle Cliff Mammal Bed; ◇ = Creechbarrow; ○ = Weissenburg 8; □ = type assemblage of *P. crusafonti* Louis & Sudre from Grisolles; △ = Perrière; ▲ = Le Bretou; ■ = Malpérié; ◆ = holotype of *P. reguanti* Crusafont-Pairo from San Cugat de Gavadons; ▽ = Eclépens [B]; ▼ = Nordshausen bei Kassel. Data from Weissenburg 8, San Cugat, Eclépens and Nordshausen from Schmidt-Kittler (1977*a*: text-fig. 11); those from Grisolles, Perrière, Le Bretou and Malpérié from Louis & Sudre (1975: tab. 7). Measurements in millimetres.

Genus ***MICROCHOERUS*** Wood 1844

TYPE SPECIES. *Microchoerus erinaceus* Wood 1844. Lower Headon Beds (early Ludian), Hordle Cliff, England.

INCLUDED SPECIES. *M. edwardsi* (Filhol 1880*a*); *M. ornatus* Stehlin 1916 (doubtfully distinct from *M. edwardsi*); *M. wardi* sp. nov.; *M. creechbarrowensis* sp. nov.; *M.* sp. from Grisolles.

RANGE. Bartonian (Marinesian) to late Ludian, England, France, West Germany, Switzerland and Spain.

EMENDED DIAGNOSIS. Tooth enamel wrinkling present; mesiolingual crest from paracone on I^1–P^4 present; P^{3-4} paracone–protocone crest may be present; P^4 metastylar wing short; upper molar *Nannopithex* fold present; M^{1-2} outline subquadrate, slightly broader than long to equidimensional; M^{1-2} hypocone nearly as large as protocone; M^{1-2} paraconule and metaconule large and metaconule double; M^{1-2} mesostyle present; I_1 broad with distolingual cingulum strong; P_{2-3} relatively moderately short with high distal cingula; M_1 trigonid length greater than talonid; M_{1-2} protocristid broken and displaced; M_{1-2} entoconid lower than metaconid; M_{1-2} hypoconulid small to large, single to double; M_3 hypoconulid lobe broad, moderately long to long, bicuspid; lower molar paracristid with paraconid on M_1, without paraconid and fusing with metaconid on M_{2-3}; angular process expanded; coronoid process low.

DIFFERENTIAL DIAGNOSIS. *Necrolemur* has no M^{1-2} mesostyle, small or absent M_{1-2} hypoconulid, smaller M^{1-2} paraconule and metaconule; and M_{1-2} protocristid is straight and complete to slightly broken and displaced and $M\frac{3}{3}$ are smaller with M_3 hypoconulid lobe usually shorter and narrower.

EVOLUTIONARY GRADE IN *Microchoerus*. Louis & Sudre (1975: 819–821) described the first recorded as well as the oldest known association of *Microchoerus* and *Necrolemur* at the same locality. They listed features which for them distinguished the two genera. They stated that a mesostyle is only sometimes present on *Microchoerus* upper molars, in contrast to most authors (e.g. Cooper 1910, Stehlin 1916, Hill 1955, Cray 1973, Schmid 1979) who have used it as a constant diagnostic feature. Study of the sample of *Microchoerus* from Grisolles in the UM has shown that, although variable in size and often weak, the mesostyle is constantly present even in this early (Marinesian) assemblage. Godinot (1985) has, however, recently documented a Ludian *Microchoerus* lineage in which the mesostyle is sometimes absent. Another character mentioned by Louis & Sudre was the greater lingual spread of the molar paracone and metacone in *Necrolemur*. Although difficult to assess, this seems to result from the smaller size of the paraconule and metaconule (the latter usually doubled) in *Necrolemur*. An examination of the occlusal relations of the upper and lower molars of *Necrolemur* and *Microchoerus* has shown that this, along with the remaining characters listed by Louis & Sudre, constitute important grade features which, however, could not entirely separate the two genera unless they occurred in association at the same locality.

These grade changes are outlined below; in each case the equivalent changes in the upper and lower teeth are placed alongside. For simplicity they are divided into two regions of the tooth: mesial and distal.

A. Mesial: M^{1-2}	M_{1-2}
1. Small paraconule, single paracone	Protocristid straight and unbroken.
2. Large paraconule, paracone single or incipiently double joined by crest.	Protocristid broken in middle, lingual half more distal than buccal half and may be confluent with cristid obliqua.
3. Large paraconule, double paracone.	Protocristid broken in middle, lingual half more distal than buccal half and may be confluent with cristid obliqua; mesoconid development on cristid obliqua.

B. Distal: M^{1-2}	M_{1-2}
1. Small metaconule, single or doubled.	Postcristid high, complete and even, without hypoconulid.
2. Large buccal metaconule and small lingual metaconule.	Postcristid lower, bent in middle just buccal to small hypoconulid.
3. Both metaconules large.	Postcristid broken by larger doubled hypoconulids.

Necrolemur zitteli is essentially at stage 1; *N. antiquus* may reach stage 2 (see also Godinot 1985); *Microchoerus erinaceus* is at stage 2 with some individuals tending towards stage 3; *M. edwardsi* has most individuals at stage 3; *M. ornatus* is at stage 3; *M. wardi* (p. 259) is at stage 2, with some tendency towards stage 3; *M. creechbarrowensis* (p. 261) is at stage 2; and *M.* sp. from Grisolles is between stages 1 and 2.

These characters indicate slight overlap in grade between late (Ludian) *Necrolemur* (*N. antiquus*) and early (Marinesian) *Microchoerus* (*M.* sp. from Grisolles). Only the presence of a mesostyle in *Microchoerus* then totally distinguishes it from *Necrolemur*. In those from Grisolles, it is a very weak structure. The evolution of *Microchoerus* from an animal with *Necrolemur*-

Table 7 Length (l) and maximum width (w) measurements of *Microchoerus* species from Creechbarrow. Measurements in millimetres.

	Microchoerus wardi			*Microchoerus creechbarrowensis*		
Tooth	No.	l	w	No.	l	w
C^1	M37159	2·00	1·80	M35428	(2·70)	1·85
	M37160	2·15	1·60	M35730	2·50	1·75
	M35742	2·30	1·60			
P^3	M35745	2·20	2·40			
P^4				M37155	2·60	3·20
M^1	M35436	2·90	3·40	M35731	3·25	(4·10)
	M35746	2·70	3·25	M35732	3·30	4·10
	M37162	2·65	3·25			
M^2	M35437	2·60	3·45	M35733	3·00	3·90
M^3	M37163	2·05	2·75	M35734	2·55	3·45
				M37156	2·50	3·00
I_1	M35747	1·70	1·65			
DI_1?	M35719	1·30	1·05			
P_2	M35439	2·25	1·55			
P_4	M35432	2·50	2·00	M37157	2·85	2·50
				M35431	2·95	2·10
				M37158	2·85	2·25
M_1	M35749	2·95	2·20			
	M37165	3·05	2·40			
M_2	M37166	2·95	2·30	M35737	3·25	2·60
	M35750	2·90	2·05			
$M_{1/2}$	M37167	–	2·15	M35739	–	(2·45)
M_3	M35752	–	1·90	M35433	–	2·55
	M35751	–	1·95			
	M35753	–	1·85			

like M^{1-2} is likely to have involved an increase in size accompanied by incipient development of a mesostyle and a molar grade change from 1 towards 2.

THE SPECIES OF *Microchoerus*. There has long been disagreement on how best to divide the genus at species level or lower, and on what criteria. *M. erinaceus* and *M. edwardsi* have been distinguished by some on size (e.g. Depéret 1917, Insole 1972) and others on degree of complication of tooth enamel by wrinkling and duplication of cusps (e.g. Stehlin 1916, Hill 1955, Cray 1973, Schmidt-Kittler 1971*b*, Louis & Sudre 1975, Schmidt-Kittler 1977*a*, Schmid 1979). In the latter case, *M. edwardsi* has often been reduced to the rank of a subspecies of *M. erinaceus*, because of overlap in the variable characters which define it for these authors. Insole (1972) considered that two distinct size groups occurred together through much of the Fluviomarine series (Ludian) of the Isle of Wight. On the basis of measurements of the type specimens, he attributed the larger one to *M. erinaceus*, the smaller to *M. edwardsi*. He considered *M. ornatus* to represent merely a variant of *M. edwardsi* in which enamel complication was extreme. At most horizons the sample sizes were low for at least one of the two species represented; but whereas the smaller form normally showed a duplicated molar paracone, the larger normally showed a single paracone (Insole 1972, text-figs 43–44, tab. 19).

This then suggested that Schmidt-Kittler's (1971*b*) evolutionary series of *M. erinaceus erinaceus* to *M. erinaceus edwardsi* was untenable, and that various small specimens from continental Europe attributed to *M. erinaceus*, or aff. or cf. to this species, have probably been misidentified. Insole's scatter diagrams also suggest that the same two size types of *Microchoerus* may have existed in continental Europe during the Ludian, but the sample sizes are very small. Further support, however, comes from rather large ranges of size and possible bimodality in some of Schmid's histograms (1979: 309, fig. 5), for instance 'Euzet/Perrière'. In this example, of course, the variation could alternatively have been increased by lumping two assemblages of slightly different ages. The coefficient of variation of Schmidt-Kittler's (1971*b*) M_1 length measurements from his *M. erinaceus edwardsi* assemblage from Ehrenstein 1A is greater than 10. Perhaps the smaller measurements belong to *Necrolemur* or a similar-sized undescribed species of *Microchoerus*.

The sample of *Microchoerus* teeth from the English Bartonian (Creechbarrow) is small, but two sizes appear to be represented. One is the size of *M. edwardsi*, the other is smaller. The M^{1-2} plot of *Microchoerus* from Grisolles, according to Louis & Sudre's (1975) measurements, is intermediate between the two from Creechbarrow (Text-fig. 23A). It is considered that, despite the small number of specimens, two species are represented at Creechbarrow, because both of the distance of size separation, and of the total size range spanned by the two (coefficient of variation of M^1 is greater than 10). They both also differ from *M. erinaceus*, *M. edwardsi* and the undescribed species from Grisolles.

Microchoerus wardi sp. nov.

(Pl. 6, figs 2–3; Pl. 7; Text-fig. 23; Tables 7–8)

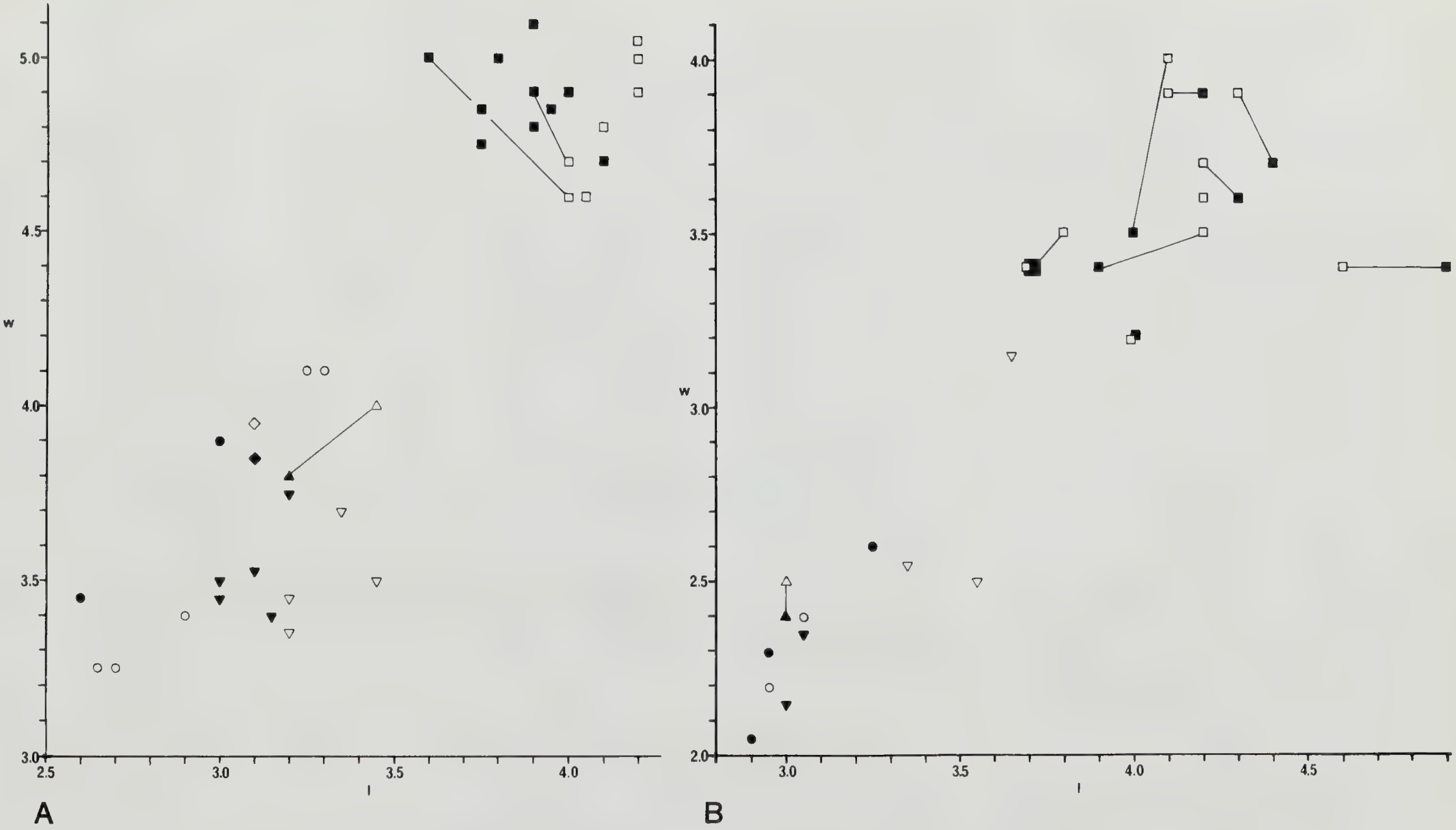
vp. *1977b* *Microchoerus* sp.; Hooker: 141.
v. *1980* *Microchoerus* sp. 1; Hooker & Insole: 38.

NAME. After Mr D. J. and Mrs A. Ward, for help with field work.

HOLOTYPE. Right M^1, M37162. Pl. 7, fig. 4.

PARATYPES. Two left upper canines (M37159–60); right upper canine (M35742); right P^3 (M35745); right P^4 protoconal fragment (M35743); two complete right M^1s and one fragment (M35436, M35746, M35435); right M^2 (M35437); left M^3 (M37163); left I_1 with tip broken (M35747); left DI_1? (M35719); right P_2 (M35439); right P_4 (M35432); left M_1 (M35749); right M_1 (M37165); left M_2 (M37166); right M_2 (M35750); right $M_{1/2}$ talonid fragment (M37167); left $M_{1/2}$ buccal fragment (M37168); three right M_3s, one lacking much of the talonid (M35752), the other two lacking the trigonid (M35751, M35753).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.



Text-figure 23 Scatter diagram of length (l) against width (w) of M^{1-2} (A) and M_{1-2} (B) of species of *Microchoerus* from various European localities: ○ = Creechbarrow (*M. wardi* and *M. creechbarrowensis* spp. nov.); □ = Lower Headon Beds, Hordle Cliff (*M. erinaceus* Wood); ◇ = Lower Headon Beds, Headon Hill (*M. edwardsi*?); ▽ = Grisolles; △ = Holotype *M. ornatus* Stehlin from Entreroches in diagram A and holotype of *M. edwardsi* (Filhol) from Quercy in diagram B. Outline symbol = $\mathrm{M}\frac{1}{1}$, solid symbol = $\mathrm{M}\frac{2}{2}$. Data for Hordle Cliff from Cray (1973), for Headon Hill from Insole (1972), for Grisolles from Louis & Sudre (1975), for Entreroches from Stehlin (1916) and for Quercy from Filhol (1880*a*). Measurements in millimetres. Lines join teeth of one individual.

DIAGNOSIS. Size small ($\bar{x}$ M^1 length = 2·75 mm). Lingual M^{1-2} metaconule usually cuspate, smaller than the buccal metaconule. Strong M^{1-2} mesostyle small to medium. Upper molar paracone sometimes double. M_{1-2} protocristid variable. M_{1-2} postcristid complete, high to slow, slightly to strongly bent in middle. M_{1-2} hypoconulid single, small to large. M_3 hypoconulid lobe nearly as large as talonid.

DESCRIPTION. The upper canine is typical for the genus in having the mesiolingual paracone crest, enclosing a triangular mesial hollow between it and the preparacrista.

The P^3 and P^4 are typical and the enamel is more wrinkled than in the *M. creechbarrowensis* P^4.

Selected important characters of M^{1-2} (other than mesostyle morphology) are indicated in Table 8 in comparison with other *Microchoerus* assemblages. The mesostyle is equidistant between paracone and metacone except on M35746, where it is slightly more distal in position and curves distally where it meets the ectocingulum, there being an ectoflexus immediately mesially. This latter specimen is more like the two M^1s of *M. creechbarrowensis*. In M35436–7 and M37162 the mesostyle is straight, forming a broad ridge which reaches or nearly reaches the ectocingulum from the median point of the centrocrista. The mesostyle on the Grisolles M^{1-2}s is generally weaker (see Table 8) but similarly ridge-like. This ridge-like shape was characterized as the most basic type of *Microchoerus* mesostyle by Schmidt-Kittler (1971*b*: 187; 'Transversalgrates'). His other two more advanced types were: looped ('Mesostyl-Schleife') and conical ('spitz-kegelförmiges'). The last two do not occur in the Creechbarrow or Grisolles assemblages as at present known, but they do occur in *M. erinaceus* from the Lower Headon Beds of Hordle Cliff.

The M^3 is broader than long with the talon only slightly expanded distal to the hypocone. The paracone is double. A small mesostyle arises from the ectocingulum and is joined by a faint ridge to a point on the centrocrista distal of the midline.

I_1 lacks the weak buccal cingulum present in two specimens of *M. erinaceus* from Hordle Cliff. The morphology is otherwise identical.

The DI_1? is very similar in overall morphology to I_1 but is much smaller, has a faint rib on the buccal wall, a faint mesiobuccal cingulum, a small talonid cusp and thinner enamel.

The P_4 fits Teilhard's (1921: text-fig. 5A) normal ('nonmolariform') type, with small median paraconid and near longitudinal paracristid. The metaconid is distinctly smaller than the protoconid and is bounded by a lingual cingulum.

For M_{1-2} see Table 8. Both the M_3s (M35751 and M35753) have a bicuspid hypoconulid lobe, which is shorter and broader in the latter than in the former. They have been compared with ten M_3s of *M. erinaceus* (including the holotype) from the Lower Headon Beds of Hordle Cliff; in all of these the lobe is narrower than in M35753. Also the distance between the entoconid and lingual hypoconulid is always less than that between the entoconid and hypoconid. Only two Hordle Cliff specimens are like M35753 in having the former distance almost as great as the latter. In M35751, the lingual hypoconulid is further away from the entoconid than is the hypoconid. Thus in length and width of the hypoconulid lobe, *M. wardi* is more like *M. edwardsi* (e.g. see Schmidt-Kittler 1971*b*: pl. 13, fig. 3; 1977*a*: 189, text-fig. 9a) than *M. erinaceus* (see Cray 1973: pl. 3, fig. 1; pl. 4, fig. 1).

Microchoerus creechbarrowensis sp. nov.

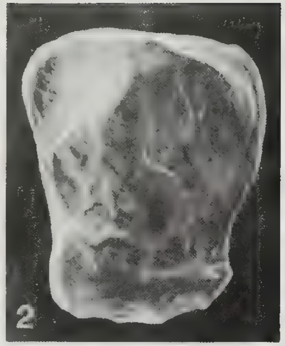
(Pl. 8; Text-fig. 23; Tables 7–8)

vp. *1977b* *Microchoerus* sp.; Hooker: 141.
v. *1980* *Microchoerus* sp. 2; Hooker & Insole: 38.

NAME. From the type locality.

HOLOTYPE. Right M^1, M35732. Pl. 8, fig. 2.

PARATYPES. Two right upper canines (M35428, M35730); left P^4 (M37155); right M^1 (M35731); right M^2 (M35733); three right M^3s, the third one fragmentary (M35734, M37156, M35735);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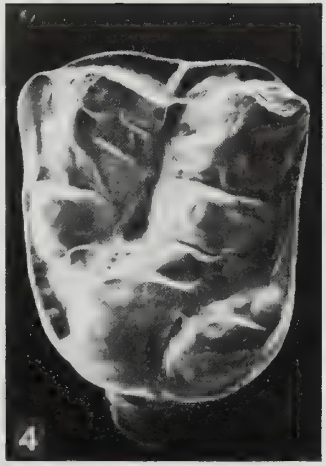
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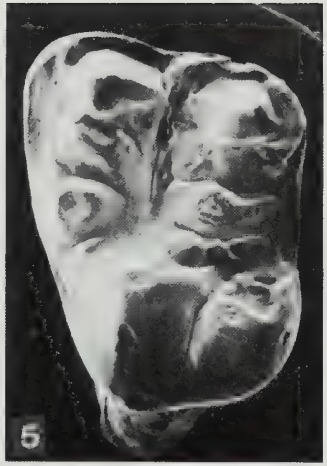
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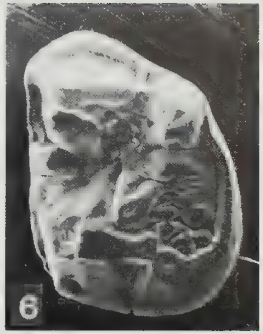
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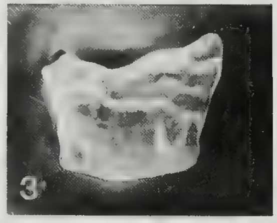
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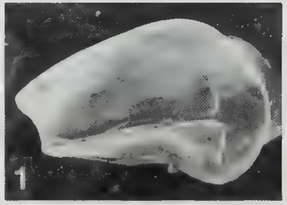
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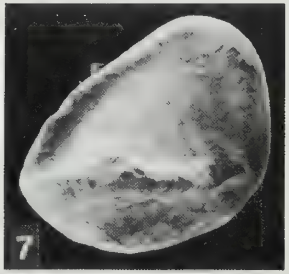
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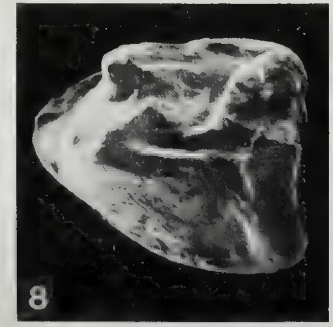
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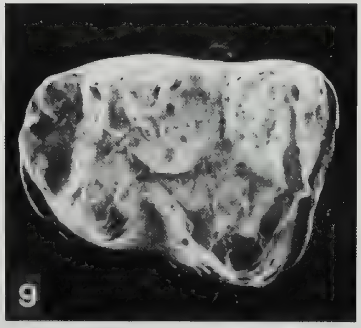
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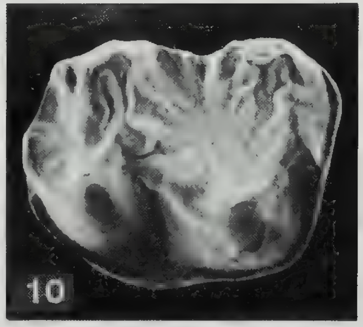
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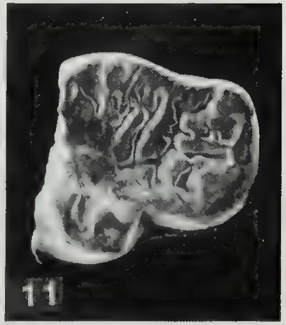
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two left P_4s (M35430, M37157); two right P_4s (M35431, M37158); left M_2 (M35737); two right $M_{1/2}$ talonid fragments (M35738–9); left M_3 (M35433).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Size medium ($\bar{x}$ M^1 length = 3·28 mm). Lingual M^{1-2} metaconule more often a transverse ridge, than a cusp smaller than the buccal metaconule. Strong M^{1-2} mesostyle medium to large. Upper molar paracone single. M_2 protocristid unbroken. $M_{1\ 2}$ postcristid high, complete, slightly broken in middle. M_{1-2} hypoconulid single, usually small. [M_3 hypoconulid lobe unknown].

DESCRIPTION. On P^4 the enamel is very weakly wrinkled; there is no hypocone but instead a small hypostyle.

Selected important characters (other than mesostyle morphology) are listed in Table 8. On both M^1s the ectocingulum is raised into a large mesostylar cusp just mesiobuccal to the metacone; a crest from its mesial end joins it to the centrocrista just distal to the midpoint. This form of mesostyle was not described by Schmidt-Kittler (1971*b*) for *M. edwardsi* from Ehrenstein 1A and does not occur in the assemblages from Grisolles or Hordle Cliff. More specimens are needed to tell whether this character has more than individual importance in the light of the wide intraspecific morphological variation usually encountered in this genus. Both specimens are too worn to compare enamel wrinkling with that of *M. wardi*. The M^2 mesostyle is a more normal transverse ridge occurring only slightly distal to the centrocrista midpoint.

One M^3 (M35734) is nearly twice as broad as long and talon expansion is similar to *M. wardi*. There is a weak distal ridge-like mesostyle. M37156, conversely, is nearly as long as broad with a much more expanded talon and the paracone and metacone are more separated than on M35734. There is no mesostyle. On both teeth the paracone is single.

Of the three complete P_4s, M37157 is like Teilhard's (1921: text-fig. 5A) normal (non-molariform) type, like *M. wardi* but without the lingual cingulum and with subequal protoconid and metaconid; whereas M35431 and M37158 are of his molarized type (1921: text-fig. 5B) with larger lingual paraconid. Paraconid and metaconid are not fused, however, as they are in Teilhard's extreme example.

For M_{1-2} see Table 8. The M_3 has its hypoconulid lobe missing. Its enamel is less wrinkled than in *M. wardi* M_3s.

PHYLOGENY OF *Microchoerus*. Insole's (1972) view of large *M. erinaceus* and small *M. edwardsi* (including *M. ornatus*) evolving in parallel through the Ludian (discussed above) is considered a more plausible working hypothesis than that of Schmidt-Kittler (1971*b*), for whom these taxa had an ancestor–descendant relationship. Of the two Creechbarrow species, the smaller *M. wardi* is more like *M. edwardsi* in the upper molar paracone and M_3 hypoconulid lobe; whereas *M. creechbarrowensis* is more like *M. erinaceus* in the upper molar paracone. Moreover, there is slight evidence that there was greater percentage tooth enamel wrinkling in *M. wardi* than in *M. creechbarrowensis*, as in *M. edwardsi* over *M. erinaceus*.

It is possible that *M. wardi* and *M. creechbarrowensis* gave rise to *M. edwardsi* and *M. erinaceus* respectively, by size increase and the relevant grade change as discussed above. It is also possible that the *Microchoerus* from Grisolles, the most primitive of any described, gave rise to both *M. wardi* and *M. creechbarrowensis*. Whereas biostratigraphical evidence from

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Plate 7 Scanning electron micrographs of occlusal views of teeth of *Microchoerus wardi* sp. nov. from Creechbarrow, × 15. Fig. 1, right upper canine (reversed) (M35742). Fig. 2, right P^3 (reversed) (M35745). Fig. 3, lingual half of right P^4 (reversed) (M35743). Fig. 4, **holotype** right M^1 (reversed) (M37162). Fig. 5, right M^2 (reversed) (M35437). Fig. 6, left M^3 (M37163). Fig. 7, right P_2 (reversed) (M35439). Fig. 8, right P_4 (reversed) (M35432). Fig. 9, left M_1 (M35749). Fig. 10, right M_2 (reversed) (M35750). Fig. 11, right M_3 lacking trigonid (reversed) (M35751). See p. 259.

other mammalian groups places both Creechbarrow and Grisolles in the Marinesian, there is no independent stratigraphical evidence on the relative position of these sites within this time period (see correlation section). The scheme in Text-fig. 25 is provisional, based on the characters observed and as far as possible on stratigraphical position.

Table 8 Number rated development states of certain variable characters of M$\frac{1}{1}-\frac{2}{2}$ of species of *Microchoerus*.

Upper molars: Mesostyle size 1, 2, 3, 4. Paracone single or double: 1, 2. Hypostyle present or absent: 0, 1. Lingual metaconule: a transverse ridge (1); smaller than buccal metaconule (2); subequal with buccal metaconule (3). Pericone present or absent: 0, 1.

Lower molars: Protocristid broken lingual half: joined to cristid obliqua (1); separate from cristid obliqua (2). Mesoconid: absent (0); one small (1); one large, not separated from hypoconid (2); two or one very large separated from hypoconid (3). Postcristid: high, complete, slightly bent in middle (1); low complete, strongly bent in middle (2); low, incomplete (3); deeply divided (4). Hypoconulid: absent (0); one small (1); one large, distinct (2); two (3).

The presence of a hypoconulid or a mesoconid is somewhat arbitrary. Enamel wrinkles in the position of these cusps, no larger than those occurring on other parts of the tooth, are not considered to constitute presence of these cusps.

Tooth	Species and Locality	No.	Mesostyle size	Paracone	Hypostyle	Lingual metaconule	Pericone	Protostyle
M^1	*M.* sp.,		1	1	0	1	1	0
	Grisolles		1	1	1	1	0	–
			1	1	0	2	1	0
			2	1	0	1	1	0
M^2			1	1	0	–	0	0
			2	1	0	1	0	0
			2	1	0	1	0	0
M^1	*M. wardi*,	M37162	2	1	1	2	0	0
	Creechbarrow	M35746	3	1	1	1	1	0
		M35436	2	1	–	2	0	0
M^2		M35437	3	2	0	2	0	0
M^1	*M. creechbarrowensis*,	M35732	4	1	1	2	1	0
	Creechbarrow	M35731	4	1	1	1	1	0
M^2		M35733	3	–	0	1	0	0
M^1	*M. erinaceus*,	M34692	–	1	1	2	0	0
	Hordle Cliff	M34694	–	–	1	2	0	0
		M34693	2	1	1	2	1	0
		M34695	3	1	1	2	0	0
		M34810	–	–	1	2	0	0
		M35038	2	1	1	2	0	1
		30346b	3	1	1	2	0	0
		30346be	2	1	1	2	0	0
		25229	3	1	?1	1	1	0
M^2		M34696	3	1	1	2	0	1
		M34698	3	1	1	2	0	0
		M34699	3	1	0	2	1	0
		M34839	3	1	1	2	0	0
		M34840	–	1	1	2	0	0
		M34811	–	–	1	2	0	0
		M34760	3	1	1	2	0	–
		M34763	2	1	–	–	–	–
		M34688	–	1	1	2	1	0
		30346b	3	1	1	2	0	0
		25229	3	?1	1	2	1	0
	M. edwardsi,							
	La Débruge	M43059	3	1	2	3	0	0
M^1	*M. ornatus*,		–	2	1	3	0	0
M^2	Entreroches (Holotype)		4	2	2	3	0	0

PHYLOGENY WITHIN THE MICROCHOERINAE. Prior to Simons' (1961) study, the genera included in the Microchoerinae were thought to be sufficiently distantly related to be placed in different subfamilies. Hürzeler (1948*b*) considered *Nannopithex* to be either lateral to *Necrolemur* or a direct ancestor and a stage in the *Necrolemur* lineage. Russell *et al.* (1967: 17) considered that *Pseudoloris* on the other hand had certain tooth characters more like some adapids than like *Necrolemur*. Szalay (1975: fig. 2) showed *Nannopithex* as a stem genus, giving rise to *Pseudoloris* and independently to *Necrolemur* and *Microchoerus* (which were included together). The

Table 8 (*continued*)

Tooth	Species and Locality	No.	Protocristid	Mesoconid	Postcristid	Hypoconulid
M_1	*M.* sp.,		1	0	1	0
	Grisolles		1	0	1	1
			1	0	1	1
M_2			2	0	1	0
			2	0	1	1
M_1	*M. wardi*,	M35749	2	1	1	1
	Creechbarrow	M37165	2	1	1	1
M_2		M35750	0	1	2	2
		M37166	2	0	?2	2
$M_{1/2}$		M37168	?1	0	–	–
		M37167	–	?1	2	2
M_2	*M. creechbarrowensis*,	M35737	0	0	1	1
$M_{1/2}$	Creechbarrow	M35738	–	–	1	1
		M35739	–	–	1	2
M_1	*M. erinaceus*,	25229	–	2	–	3
	Hordle Cliff	30346b	2	1	–	–
		30346b	2	1	3	3
		30346b	2	?1	2	?3
		M35036	2	0	2	2
		M12565	2	2	3	3
		M12563	2	2	3	3
		30338	2	0	1	1
		30346	2	2	2	3
		M34816	2	2	3	2
		M34704	2	1	2	2
		M34714	2	2	3	2
		M34717	2	2	2	2
M_2		25229	–	1	–	2
		30346b	2	1	3	3
		30346b	2	1	2	3
		M35037	2	0	3	3
		M12565	2	2	3	3
		M12563	2	2	3	3
		30346	2	1	2	2
		M34830	0	0	2	3
		M34705	2	1	2	2
		M34707	2	1	3	2
		M34708	0	0	2	2
		M34712	2	2	3	3
		M34713	2	1	2	2
		M34714	2	1	3	2
		M34716	2	1	2	2
		M34717	2	1	2	2
$M_{1/2}$		M34817	–	–	3	3
M_1	*M. edwardsi*,	Qu10946	–	3	3	3
M_2	Quercy	Qu10946	2	3	4	3

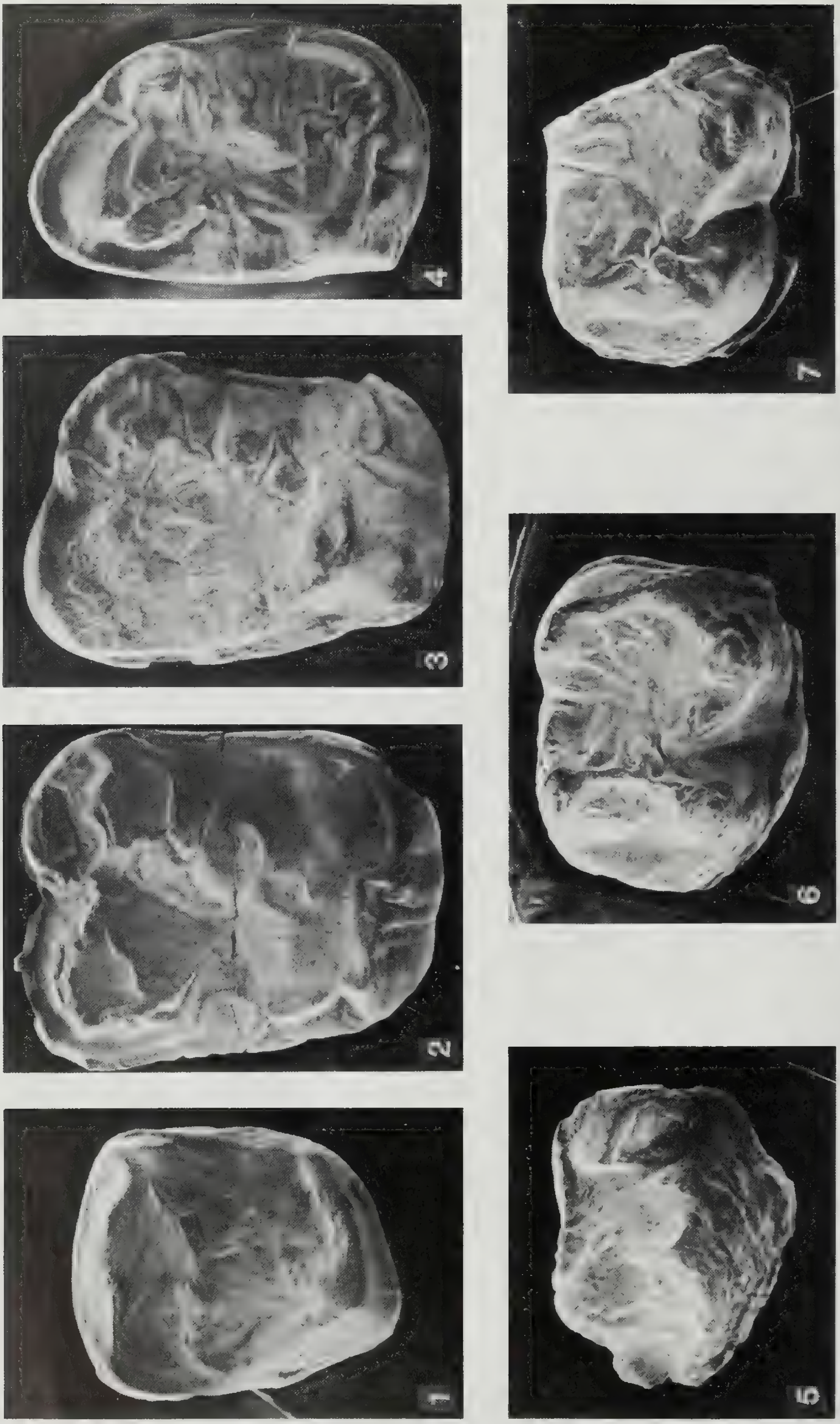


Plate 8 Scanning electron micrographs of occlusal views of teeth of *Microchoerus creechbarrowensis* sp. nov. from Creechbarrow, × 15. Fig. 1, left P^4 (M37155). Fig. 2, **holotype** right M^1 (reversed) (M35732). Fig. 3, right M^2 (reversed) (M35733). Fig. 4, right M^3 (reversed) (M35734). Fig. 5, left P_4 (M35431). Fig. 6, left M_2 (M35737). Fig. 7, left M_3 lacking hypoconulid lobe (M35433). See p. 261.

characters given above in the diagnoses for the different genera suggest that *Necrolemur* and *Microchoerus* differentiated at a later time than did *Pseudoloris*. Perhaps *Pivetonia isabenae*, if distinct from *Nannopithex*, was connected with the derivation of *Pseudoloris*.

Simons (1961: 62–63) stated: 'At present specimens of *Nannopithex* have been recovered near Egerkingen in Switzerland, at Buchsweiler in Alsace, and in the Geisel valley near Halle, Germany. *Nannopithex* does not occur in the Quercy phosphorites of Bartonian and Ludian age. Its absence at this later period reinforces the idea based on morphology that a species of this genus could have given rise to *Necrolemur*'. The Creechbarrow records of two species of *Nannopithex* extend the range of the genus into the Bartonian, where it is associated with two species of *Microchoerus* and is contemporaneous with *Necrolemur*. This need not invalidate the evolutionary scheme envisaged. Some specimens of *Nannopithex filholi* from Egerkingen γ and the Huppersand (e.g Hürzeler 1948*b*: 17, fig. 8; 22, fig. 14) show characters overlapping slightly with *Necrolemur*. These characters are a larger M^1 hypocone and a bicuspid M_3 hypoconulid lobe. *Nannopithex*, with as many of its generic characters as are known, continues into the Bartonian with only minor differences from the Lutetian species. Although it is accepted that *Nannopithex* is paraphyletic, its concept as a microchoerine stem genus is a useful one and it is retained for this reason. See Table 9 and Text-figs 24–25 for character table, cladogram and phylogeny, where primitive versus advanced states have been calculated by outgroup comparison with the rest of the Omomyidae.

Infraorder **LEMURIFORMES** Gregory 1915

Family **ADAPIDAE** Trouessart 1879 (*sensu* Hill 1953)

Subfamily **ADAPINAE** Trouessart 1879

(nominate subfamily *sensu* Hill 1953)

TYPE GENUS. *Adapis* Cuvier 1822.

INCLUDED GENERA. *Donrussellia* Szalay 1976, *Pronycticebus* Grandidier 1904, *Protoadapis* Lemoine 1880, *Europolemur* Weigelt 1933, *Cercamonius* Gingerich 1975*c*, *Caenopithecus* Rütimeyer 1862, *Periconodon* Stehlin 1916, ?*Agerinia* Crusafont-Pairo & Golpe-Posse 1975 (= *Agerina* Crusafont-Pairo 1967), *Anchomomys* Stehlin 1916 (?including *Huerzeleris* Szalay 1974), *Microadapis* Szalay 1974, *Leptadapis* Gervais 1876, *Cryptadapis* Godinot 1984, *Mahgarita* Wilson & Szalay 1977 (= *Margarita* Wilson & Szalay 1976, *non* Leach 1814 &c.), *Indraloris* Lewis 1933 and *Sivaladapis* Gingerich & Sahni 1979.

RANGE. Sparnacian–Stampian, Europe; Uintan, U.S.A.; Late Miocene, India.

DIAGNOSIS. See Cray (1973: 65) under Adapidae.

Genus ***EUROPOLEMUR*** Weigelt 1933

[= *Megatarsius* Weigelt 1933 and *Alsatia* Tattersall & Schwartz 1984]

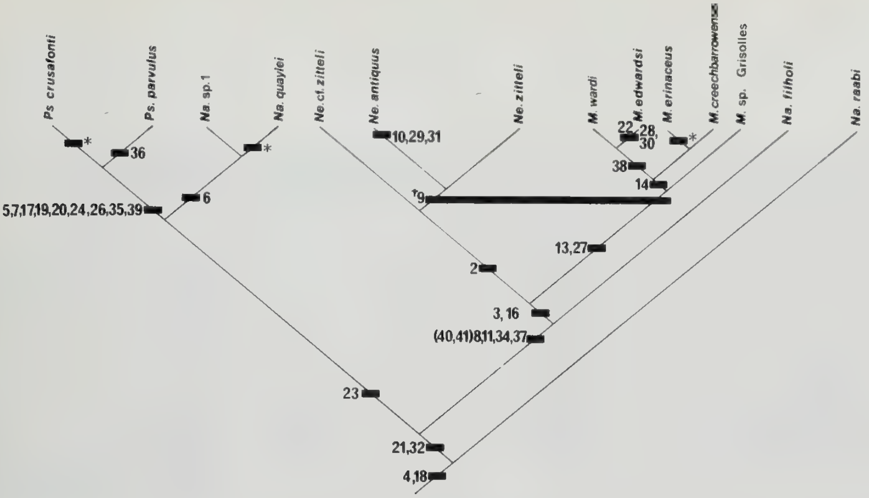
TYPE SPECIES. *E. klatti* Weigelt 1933. Lower Brown Coal, Leonhardt Mine, Geiseltal, D.D.R.

INCLUDED SPECIES. *E. collinsonae* sp. nov., *E.* aff. *klatti*.

RANGE. Early Lutetian, D.D.R.; Middle Lutetian, France; Late Lutetian, Switzerland; Bartonian, England.

EMENDED DIAGNOSIS. Medium to large adapine; dental formula $\frac{2\ 1\ 3\ 3}{2\ 1\ 3\ 3}$; canines large and pointed; upper molars without pericone or postflexus, with strong postprotocrista lacking metaconule; M^3 smaller and relatively shorter than M^2; P^4 much shorter than broad with weak parastyle; P_4 with small unicuspid talonid and metaconid present to absent; M_{1-2} protocristid and postcristid nearly transverse.

	Character	State		*Na. raabi*	*Na. filholi*	*Na. quaylei* and sp. 1	*Ps. parvulus*	*Ps. crusafonti*	*Ne.* cf. *zitteli*	*Ne. zitteli*	*Ne. antiquus*	*M.* sp. (Grisolles)	*M. wardi*	*M. creechbarrowensis*	*M. erinaceus*	*M. edwardsi*
		primitive	advanced													
1	Enamel wrinkling	no	yes	+/–	+	–	–	–	+	+	+	+	+	+	+	+
2	M3	not reduced	reduced	–	–	–	–	–	+	+	+	–	–	–	–	–
3	Mesiolingual paracone crest	no	yes	–	–	–	–	–	+	+	+	+	+	+	+	+
4	I^2 reduction	slight	great	+	?+	?+	+	?+	+	+	+	+	+	+	+	+
5	P^4 metastylar wing	short	long	–	–	–	+	+	–	–	–	–	–	–	–	–
6	P^4 parastyle	weak	strong	–	–	+	–	–	–	–	–	–	–	–	–	–
7	Upper molar *Nannopithex* fold	yes	no	–	–	–	+	+	–	–	–	–	–	–	–	–
8	M^{1-2} outline	subtriangular	subquadrate	–	+/–	–	–	–	+	+	+	+	+	+	+	+
9	M^1 width	>length	=length	–	–	–	–	–	–	+	+	+	+	+	+	+
10	M^{1-2} paraconule and metaconule	small	large	–	–	–	–	–	–	–	+/–	+/–	+	+	+	+
11	M^{1-2} metaconule	single	double	–	+/–	–	–	–	+/–	+/–	+/–	+	+	+	+	+
12	M^{1-2} paracone	single	double	–	–	–	–	–	–	–	+/–	–	+/–	–	+/–	+
13	M^{1-2} mesostyle	no	yes	–	–	–	–	–	–	–	–	+	+	+	+	+
14	Mesostyle strength	weak	strong									–	+	+	+	+
15	M^{1-2} hypocone	weak	strong	–	+/–	–	+	–	+	+	+	+	+	+	+	+
16	I_1 width	narrow	broad	–	?	–	–	?–	?+	+	+	+	+	?+	+	+
17	I_1 distolingual cingulum	strong	weak	–	?–	–	+	?+	–	–	–	–	–	?–	–	–
18	Lower canine reduction	slight	great	+	?+	?+	+	?+	?+	+	+	?+	?+	?+	+	+
19	P_{2-3} distal cingulum	high	low	–	–	–	+	?+	–	–	–	–	–	?–	–	–
20	P_{2-3} l/w proportions	c. 1	>1	–	–	–	+	?+	–	–	–	–	–	?–	–	–
21	P_3 roots	sometimes 2	always 1	–	+	+	+	?+	+	+	+	+	?+	?+	+	+
22	Lower molar mesoconid	no	yes	–	–	–	–	–	–	–	–	–	+/–	–	+/–	+
23	M_1 trigonid length	>talonid	=talonid	–	–	+	+	+	–	–	–	–	–	–	–	–
24	M_1 paraconid	yes	no	–	–	?–	+	+	–	–	–	–	–	–	–	–
25	M_2 paraconid	yes	no	–	+/–	?–	+	+	+	+	+	+	+	+	+	+
26	M_{1-2} entoconid height	<metaconid	=metaconid	–	–	?–	+	+	–	–	–	–	–	–	–	–
27	M_{1-2} hypoconulid	variable	constant	–	–	–	–	–	–	–	–	+	+	+	+	+
28	M_{1-2} hypoconulid	single	usually double	–	–	–	–	–	–	–	–	–	–	–	+/–	+
29	M_{1-2} postcristid	straight	bent in middle	–	–	–	–	–	–	–	+/–	+/–	+	+	+	+
30	M_{1-2} postcristid	unbroken	broken	–	–	–	–	–	–	–	–	–	–	–	+/–	+
31	M_{1-2} protocristid	straight	displaced	–	–	–	–	–	–	–	+/–	+/–	+	+	+	+
32	M_3 paraconid	maybe present	absent	–	+	?+	+	+	+	+	+	+	+	+	+	+
33	M_3 hypoconulid lobe	short	long	–	+/–	+	–	–	+/–	+/–	+/–	+	+	+	+	+
34	M_3 hypoconulid lobe	narrow	broad	–	+/–	–	–	–	+/–	+/–	+	+	+	+	+	+
35	M_3 hypoconulid lobe	unconstricted	constricted	–	–	–	+	+	–	–	–	–	–	–	–	–
36	M_3 hypoconulid constriction	weak	strong				+	–								
37	M_3 hypoconulid lobe	unicuspid	bicuspid	–	+/–	–	–	–	+/–	+	+	+	+	+	+	+
38	Broad hypoconulid lobe	not inflated	inflated		–				–	–	–	–	+	–	–	+
39	M_3 paracristid – metaconid	joined	not joined	–	–	?–	+	+	–	–	–	–	–	–	–	–
40	Angular process expansion	no	yes	–	?+	?	–	?–	?+	+	+	?+	?+	?+	+	+
41	Coronoid process	high	low	–	?+	?	+	?+	?+	+	+	?+	?+	?+	+	+



Text-figure 24 Cladogram of species of the omomyid subfamily Microchoerinae. This is probably one of the most parsimonious possibilities but has not been subjected to computer analysis. Some characters are unknown for a few species only (e.g. *Ps. crusafonti*, *Na. filholi*, *Na. quaylei*), whilst others are generally poorly known (e.g. 40, 41). For instance, characters 40 and 41 are known in most species of *Necrolemur* and *Microchoerus* but it is not known whether they were incipiently developed in *Na. filholi* like characters 8, 11, 34 and 37. *Na. filholi* appears to be very variable morphologically (see Hürzeler 1948*b*), some individuals differing little from *Na. raabi*, while others show marked trends towards *Necrolemur* and *Microchoerus*. At terminal or near terminal branchings, often only size (the larger indicated by *) or a parallelism (†) are available as advanced character states. The large number of characters separating *Pseudoloris* from the rest might indicate a more distant relationship for this genus or alternatively a lack of intermediates. The correct alternative might become apparent from a detailed study of all three omomyid subfamilies and a better knowledge of *Pivetonia*. Abbreviations: *M.* = *Microchoerus*; *Na.* = *Nannopithex*; *Ne.* = *Necrolemur*; *Pi.* = *Pivetonia*; and *Ps.* = *Pseudoloris*. Character numbers are identified in Table 9, opposite.

DIFFERENTIAL DIAGNOSIS. *Protoadapis* differs in having M^{1-2} with small metaconules, P^4 with large parastyle and P_4 with constant metaconid.

Cercamonius has P_4 with metaconid and P_2 greatly reduced.

Mahgarita has M^{1-2} metaconule, P^2_2 greatly reduced, P^3 with reduced protocone.

Pronycticebus and *Donrussellia* have large P^4 parastyle, transversely elongated M^{1-2} with metaconules and P_4 with metaconid and bicuspid talonid.

Periconodon has M^{1-2} metaconule and pericone and weak, distally placed P_4 metaconid.

Agerinia has strong P_4 metaconid and $P_3 = P_4$ in height.

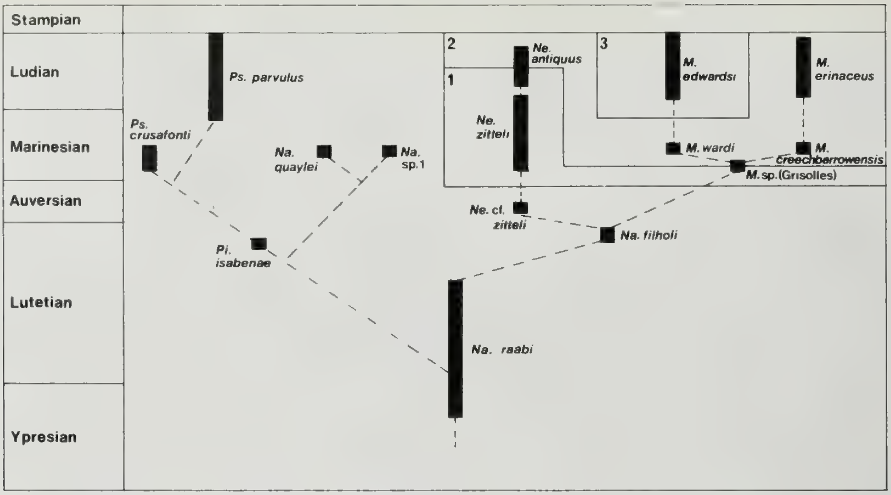
Anchomomys is smaller, has M^{1-2} postflexus and oblique protocristid and postcristid.

Microadapis has M^1 metaconule, P_4 metaconid.

Adapis, *Cryptadapis* and *Leptadapis* have weak M^{1-2} postprotocrista and nearly molariform P^4_4.

DISCUSSION. Weigelt (1933: 123) described the type species in detail but gave no formal generic diagnosis. Simons (1962: 12–14) revised the type species, placing it in *Protoadapis*, whose upper

Table 9 Characters and character states of species in the Microchoerinae. Characters are estimated as primitive (−) or advanced (+) based on outgroup comparison with the rest of the Omomyidae. '?' indicates lack of information on a character. *Na.* = *Nannopithex*; *Ps.* = *Pseudoloris*; *Ne.* = *Necrolemur*; *M.* = *Microchoerus*.



Text-figure 25 Phylogenetic model for Microchoerinae, derived from the cladogram in Text-fig. 24 (p. 269) and from stratigraphical occurrences. The numbers refer to the grades described for *Microchoerus* (p. 257) and also as they affect *Necrolemur*. Their limits are arbitrary as they exhibit gradual changes, and in some cases do not coincide with recognized species boundaries. In the case of *M*. sp. from Grisolles this is because the assemblage exhibits a grade intermediate between 1 and 2. In the case of *N. antiquus* Filhol, the change from *N. zitteli* Schlosser to *N. antiquus* reflects other changes; moreover, known specimens of *N. antiquus* are mainly from the old collections of the Quercy Phosphorites, involving mixed assemblages in which both grades 1 and 2 occur. For abbreviations see Text-fig. 24.

dentition was then unknown. Russell *et al.* (1967: 38) used absence of an M^1 ('M_1' in Russell *et al.* must be an error) metaconule as a specific character of '*P.*' *klatti*. Wilson & Szalay (1976) resurrected *Europolemur* for the type species.

Simons (1962: 12), Russell *et al.* (1967: 38) and Szalay & Delson (1979: 125) all quoted an M_{1-2} hypoconulid as a distinctive feature of *E. klatti*. The two available specimens with lower teeth lack this cusp, although there is a buccally oblique ridge running down the distal postcristid wall. Its absence has been omitted from the generic diagnosis herein because *E. collinsonae* does have a M_{1-2} hypoconulid.

The variable occurrence of a P_4 metaconid in *E. klatti* (present in Simons' (1962: pl. 3, fig. F), absent in Szalay & Delson's (1979: fig. 57B, D–E) figures) is considered to represent the beginning of an important trend in simplifying P_4, carried a stage further in *E. collinsonae* below.

With the description of the new species below, *Europolemur* is no longer monotypic, Gingerich's (1977*a*: 61) main reason for reuniting *E. klatti* with *Protoadapis*, and it is easier to understand the importance of its generic characters.

Europolemur collinsonae sp. nov.
(Pl. 9, figs 3–4; Pl. 10; Table 10)

v. *1977b* ?*Caenopithecus* sp.; Hooker: 141.
v. *1980* ?*Protoadapis* sp.; Hooker & Insole: 31, 38.

NAME. After Dr M. E. Collinson for her help with field work and other aspects of this project.

HOLOTYPE. Left M^2, M37169. Pl. 9, fig. 3.

PARATYPES. Left M^3 (M35440), right M^3 (M37170), left P_4 (M37171), two right M_1s with incomplete talonids (M35755, M37173), right M_2 (M35756), right $M_{1/2}$ talonid fragment (M37172), two left M_3s, one a trigonid fragment (M35757, M37693).

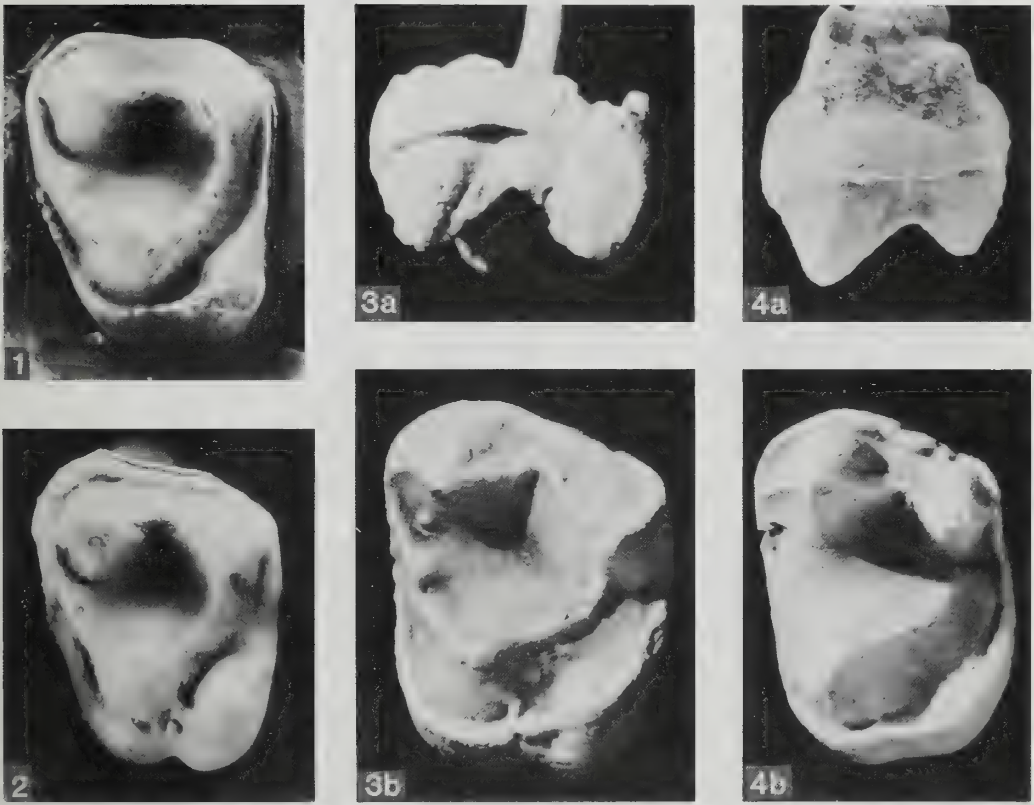


Plate 9 Light macrographs of upper molars of *Europolemur*, × 8. Figs 3a and 4a are buccal views, the rest occlusal.

Fig. 1 *Europolemur klatti* Weigelt from Bouxwiller, France. Cast of right M^2 (reversed) (NMB Bchs648; holotype of synonym, *Alsatia dunaifi* Tattersall & Schwartz 1984).

Fig. 2 *Europolemur* aff. *klatti* Weigelt from Egerkingen γ, Switzerland. Cast of right M^2 (reversed) (NMB unnumbered; BM(NH) cast no. M42083).

Figs 3, 4 *Europolemur collinsonae* sp. nov. from Creechbarrow. Fig. 3a, b, **holotype** left M^2 (M37169). Fig. 4a, b, right M^3 (reversed) (M37170). See opposite.

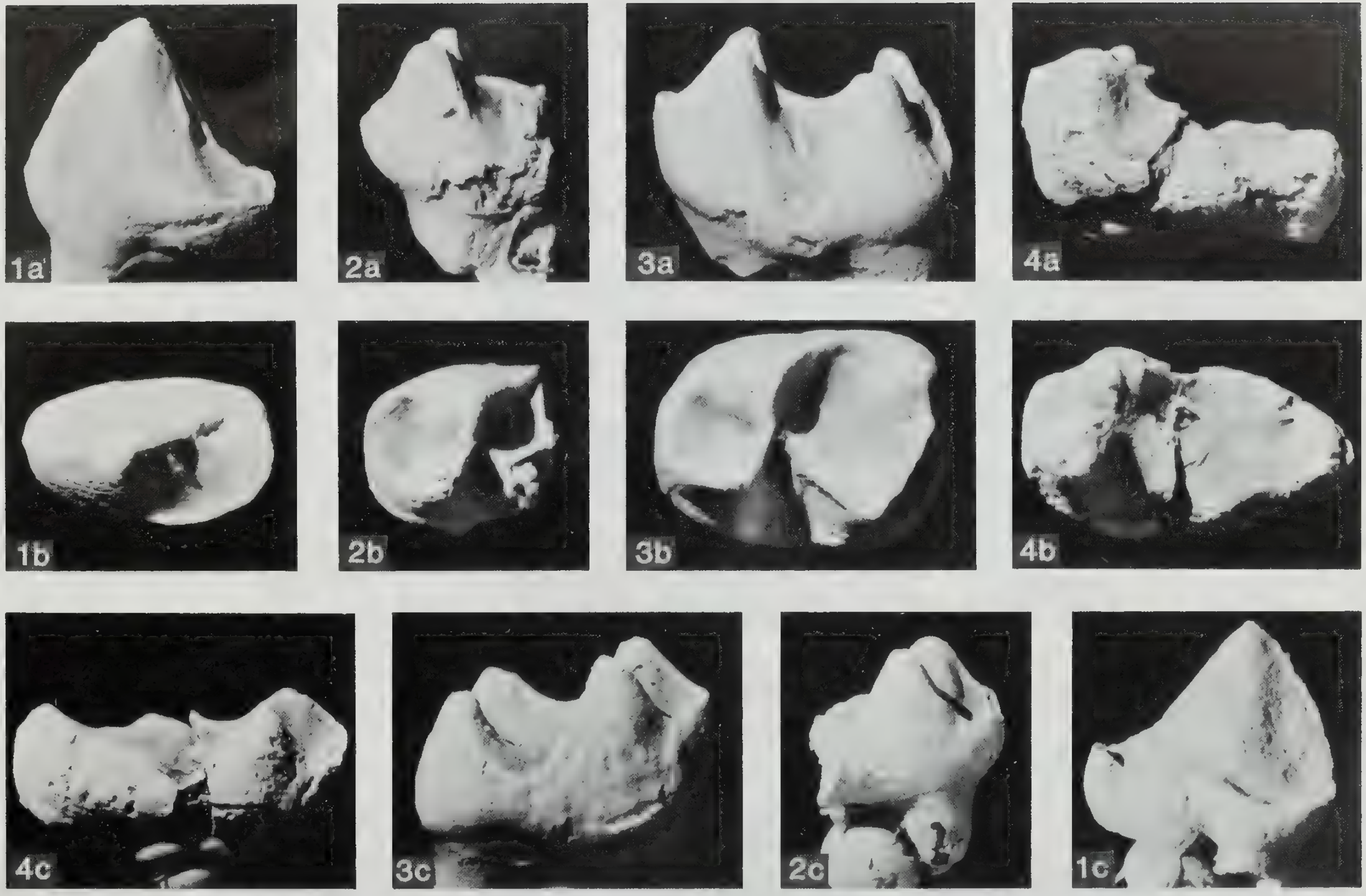


Plate 10 Light macrographs of lower cheek teeth of *Europolemur collinsonae* sp. nov. from Creechbarrow, × 8. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, left P_4 (M37171). Fig. 2a–c, right M_1 with incomplete talonid (reversed) (M35755). Fig. 3a–c, right M_2 (reversed) (M35756). Fig. 4a–c, left M_3 (M35757). See p. 270.

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Large *Europolemur* (M^2 length 4·9 mm); M^2 with hypocone nearly as tall as protocone, centrocrista buccally flexed, postprotocrista distally arched and metacone as far from paracone as is protocone; M^3 with small hypocone; P_4 with postprotocristid essentially straight, ending just short of distolingual corner, and without paraconid or metaconid; M_{1-2} with entoconid distal to and nearly as tall as hypoconid and with hypoconulid present.

DIFFERENTIAL DIAGNOSIS. *E. klatti* is slightly smaller, M^2 with smaller hypocone, straight centrocrista, only slightly distally arched postprotocrista and metacone closer to paracone than is protocone; M^3 lacks hypocone; P_4 with metaconid or with postprotocristid kinked at midpoint in position of absent metaconid and with very small paraconid; M_{1-2} with lower entoconid, which is transversely opposite hypoconid, and without hypoconulid.

DESCRIPTION. Because of the small number of specimens, documentation of variation is restricted to M^3, M_1 and M_3 (two specimens of each).

Of the M^3s, M37170 (Pl. 9, fig. 4) is broader lingually than M35440, which is triangular in shape, and its hypocone appears larger, although M35440 is more worn. The crown base of the hypocone is drawn out into a point lingually on M35440 over a transversely elongated and mesiodistally short lingual root.

M_1 can be distinguished from M_2 by having a longer trigonid which is angled instead of bevelled mesiolingually (Pl. 10, figs 2–3). There is no paraconid. On both M_1s the buccal cingulum is stronger than on the M_2, probably an individual difference.

The only complete M_3 (Pl. 10, fig. 4) is considerably worn but shows the presence of an entoconid smaller than the hypoconid. The tooth as a whole is narrower than the M_2 and is only very slightly larger than a topotype *E. klatti* M_3 (GH XXII/7-1961) (see Szalay & Delson 1979: 124, fig. 57B, D–E).

PHYLOGENY. A right M^2 (NMB unnumbered, cast in BM(NH) no. M42083) of *Europolemur* from Egerkingen γ is intermediate in morphology between *E. klatti* from Geiseltal and Bouxwiller and *E. collinsonae* from Creechbarrow. It is the same size as *E. klatti* but has a hypocone nearly as large as in *E. collinsonae*; its postprotocrista is slightly more distally arched than in *E. klatti*; the buccal flexing of its centrocrista is intermediate between the two species; and in the remaining characters it is similar to *E. klatti* (see Pl. 9, figs 1–3). It is thus best referred to as *E.* aff. *klatti*, but if more material should be found it may be shown to belong to a new species. It is also intermediate in time between *E. klatti* and *E. collinsonae* and it is likely that the three represent an evolving lineage. Some of the trends are similar to those which produced the

Table 10 Length (l) and mesial (w_1) and distal (w_2) width measurements of *Europolemur collinsonae* from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M37160	LM^2	4·9	6·2	
M35440	LM^3	4·2	(6·7)	
M37170	RM^3	4·1	6·1	
M37171	LP_4	4·2	2·5	
M35755	RM_1	–	(2·9)	–
M37173	RM_1	–	(2·8)	–
M35756	RM_2	5·1	3·5	3·7
M37172	R$M_{1/2}$	–	–	3·9
M35757	LM_3	5·6	3·0	2·9
M37693	LM_3	–	2·8	–

Lutetian *Caenopithecus*, with which *E. collinsonae* was first confused (Hooker 1977*b*). In particular, the buccal flexing of the centrocrista, unlike that of *Caenopithecus*, did not go as far as development of a mesostyle, nor did M$\frac{3}{3}$ expand, nor lower molar metastylids form. Instead the hypocone grew larger and the reduction of P_4 was different in aspect (Pl. 10, fig. 1), the metaconid being lost instead of being shifted lingually, and the protoconid remaining high. Both *Europolemur* and *Caenopithecus* probably share a common ancestry in *Protoadapis* (see Gingerich 1977*a*: 77, fig. 8).

Genus ***LEPTADAPIS*** Gervais 1876

[incl. *Paradapis* Tattersall & Schwartz 1984 and ?*Arisella* Crusafont-Pairo 1967]

Type species. *Adapis magnus* Filhol 1874. Phosphorites du Quercy, Raynal, France.

Included species. *L. ruetimeyeri* Stehlin 1912, *L. priscus* (Stehlin 1916) Szalay & Delson 1979, *L. stintoni* (Gingerich 1977*a*) Schwartz & Tattersall 1985, *L*? *capellae* (Crusafont-Pairo 1967) ?Szalay & Delson 1979.

Range. Bartonian–Stampian, England; ?Bartonian–late Ludian, France; late Lutetian–Auversian, Switzerland; ?Lutetian, Spain; Ludian, W. Germany.

Emended diagnosis. Medium to large adapine; dental formula $\frac{2\ 1\ 4\ 3}{2\ 1\ 4\ 3}$, canines large and pointed, uppers with apically converging ridges and grooves, lowers slightly procumbent; incisors and P$\frac{1}{1}$ reduced (P$\frac{1}{1}$ half the linear dimensions of P$\frac{2}{2}$); P$\frac{4}{4}$ semimolariform; upper molar postprotocrista weak and without metaconule; M_{1-2} hypoconulid median and postcristid slightly oblique; M_3 normally without entoconid; facial region of cranium nearly as high as long; mandibular ramus of approximately equal depth front to back.

Differential diagnosis. *Microadapis* differs in having large hypocone and paraconule and metaconule on M^1 and large entoconid on M_3. *Cryptadapis* has slightly narrower lower cheek teeth and upper molars with slightly larger hypocone.

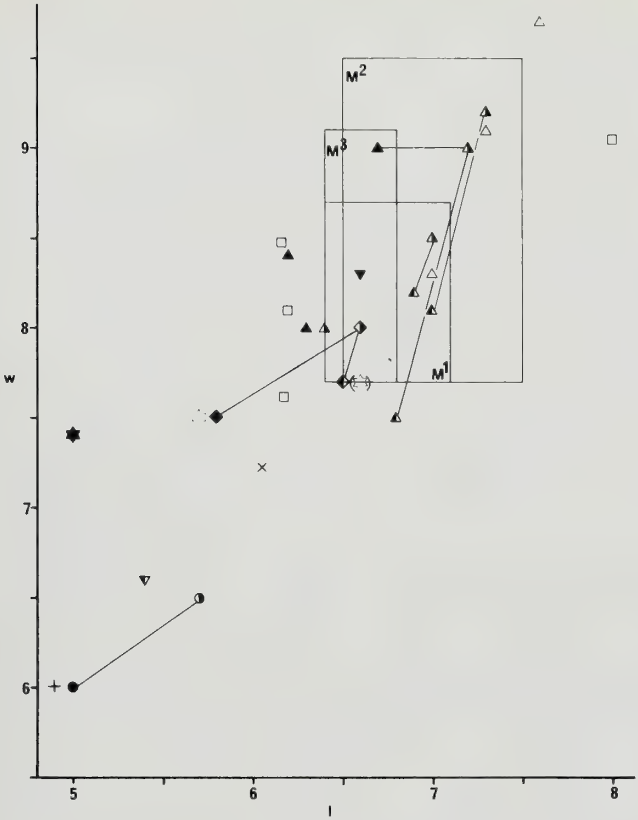
Adapis has smaller canines, the uppers ungrooved and buccolingually compressed, the lowers with a mesially sloping crested tip; incisors and P$\frac{1}{1}$ not reduced (P$\frac{1}{1}$ nearly as large as P$\frac{2}{2}$); M_{1-2} hypoconulid close to entoconid and postcristid strongly oblique; M_3 often with small sharp entoconid; facial region of cranium much lower than long; mandibular ramus deepening posteriorly.

All other adapines (where relevant parts are known) have strong upper molar postprotocrista and non-molariform P$\frac{4}{4}$.

Discussion. *Leptadapis* has been used much less frequently as a genus for the species *L. magnus* than has *Adapis*, probably because it is evidently closely related and the number of species involved is small. Sometimes *Leptadapis* has been used as a subgenus of *Adapis* (e.g. Stehlin 1912; Gingerich 1975*b*). More recently Szalay (1974: 131–132) has supported separation of the two as genera, with a brief functional analysis of the slightly different anterior dentitions. Gingerich (1977*a*: 71–72, figs 2, 5) described *Adapis stintoni* as both a morphological and stratigraphical intermediate between *A. magnus* and *A. parisiensis*, thus providing reasons for synonymizing *Leptadapis* with *Adapis*. Gingerich (1977*b*, 1981) reiterated his view of the *A. magnus* → *A. stintoni* → *A. parisiensis* lineage but also noted (1977*b*: 171) a personal communication from Sudre that two sizes of *Adapis* occurred in the French locality of Pont d'Assou (Tarn), which if confirmed would thus contradict his evolutionary scheme.

An examination of the holotype (M32135) has shown that '*A.*' *stintoni* resembles referred *L. magnus* specimens in that its mandible is uniformly shallow from front to back, and in its large lower canine and small P_1 (judged from alveoli), almost transverse lower molar postcristids and mesial P_4 metaconid. It is thus here referred to *Leptadapis*. It should not be synonymized with *A. parisiensis* as Szalay & Delson (1979: 139) have done. (Note that while this paper was in press, Schwartz & Tattersall (1985: 92) also recombined '*A.*' *stintoni* with *Leptadapis*.)

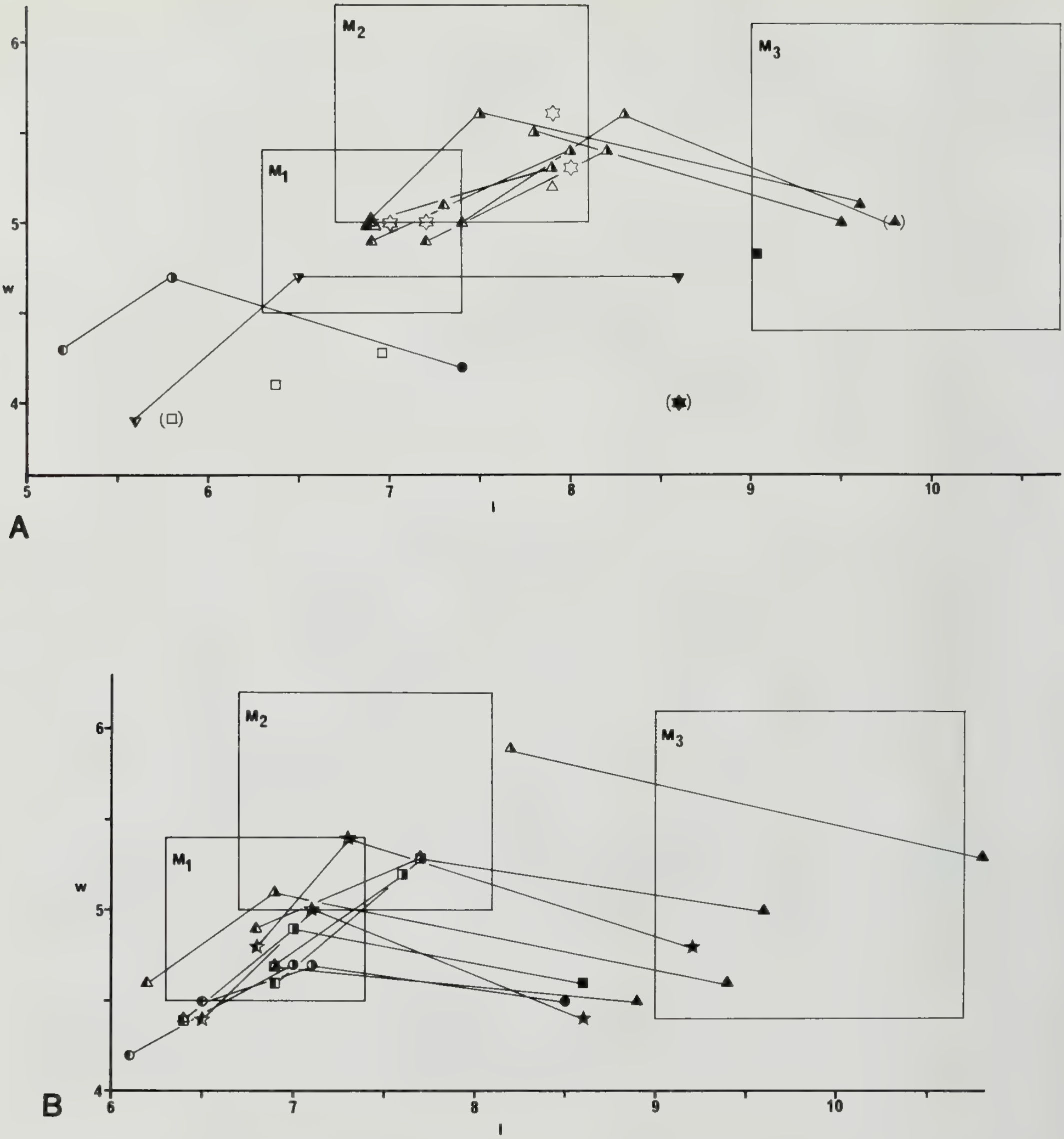
The realization that '*A.*' *stintoni* is in reality a *Leptadapis* led me to check further lines of evidence bearing on the contrasting classifications and phylogenies. Two sizes of *Leptadapis*



Text-figure 26 Scatter diagram of length (l) against width (w) of upper molars of species of *Leptadapis* from various European localities: ✩ = Creechbarrow; △ = Lower Headon Beds, Hordle Cliff; ▽ = Lignite Bed, Headon Hill Limestone, Headon Hill, the smaller plot belonging to the holotype of *L. stintoni* (Gingerich); × = Lacey's Farm Quarry; + = Lower Hamstead Beds, Bouldnor Cliff; □ = Ehrenstein 1A; ◇ = holotype of *L. magnus* (Filhol) from the Quercy Phosphorites; ○ = a syntype of *L. ruetimeyeri* Stehlin (NMB Ef417) from Egerkingen α. Large rectangles span length and width measurements obtained by Gingerich (1977*b*) from Euzet. Symbols solid on left = M^1, on right = M^2 and completely solid = M^3; outline symbols = M$^{1/2}$. Data for Lacey's Farm Quarry from Insole (1972), for Ehrenstein 1A from Schmidt-Kittler (1971*b*) and for the Phosphorites from a cast. Measurements in millimetres. Lines join teeth of one individual.

appear to occur together at three further localities: 1, Ehrenstein 1A (see Text-fig. 26 and Schmidt-Kittler's (1971*b*) upper molar measurements); 2, the lignite bed in the Headon Hill Limestone (the type locality of *L. stintoni*), where a large M^3 (M20204) has been found (see Text-fig. 26); and 3, the Lower Headon Beds, where *L. magnus* occurs at Hordle Cliff and a much smaller incomplete M$^{1/2}$ from HH2 at Headon Hill. Insole (1972: 204–205, pl. 7, fig. 2) recorded as M$^{1/2}$, small enough to belong to *L. stintoni*, from the Osborne Beds of Lacey's Farm Quarry, Isle of Wight, as *A. magnus* (see Text-fig. 26). An even smaller M$^{1/2}$ has been found in the post-Grande Coupure Lower Hamstead Beds of Bouldnor Cliff (R.L.E. Ford private collection).

Acquisition of a lower molar metastylid (Text-fig. 43) appears to have stratigraphical importance (see below). Its variable occurrence in *Leptadapis* specimens from the Quercy Phosphorites housed in the BM(NH) seemed to have the potential for providing further evidence. Text-fig. 27B shows a scatter diagram of lower molars from this collection separated on



Text-figure 27 A, scatter diagram of length (l) against width (w) of lower molars of species of *Leptadapis* from various European localities: ☆ = Creechbarrow; △ = Lower Headon Beds, Hordle Cliff; ▽ = holotype of *L. stintoni* (Gingerich) from the Lignite Bed, Headon Hill Limestone, Headon Hill; ☐ = Ehrenstein 1A; ○ = a syntype of *L. ruetimeyeri* Stehlin (NMB Ef401) from Egerkingen α. Large rectangles span length and width measurements obtained by Gingerich (1977*b*) from Euzet. Symbols solid on left = M_1, on right = M_2 and completely solid = M_3; outline symbols = $M_{1/2}$. Data for Ehrenstein 1A from Schmidt-Kittler (1971*b*). B, Scatter diagram of length (l) against width (w) of lower molars of species of *Leptadapis* from the Quercy Phosphorites in the BM(NH): ☆ = without metastylid as in the Creechbarrow assemblage; △ = with small metastylid as in the Hordle Cliff assemblage; ☐ = with large metastylid as in the Headon Hill Limestone or Ehrenstein 1A assemblages; ○ = with metastylid intermediate between Creechbarrow and Hordle Cliff assemblages. Large rectangles span length and width measurements obtained by Gingerich (1977*b*) from Euzet to facilitate comparison with A. Symbols solid on left = M_1, on right = M_2 and completely solid = M_3. Measurements in millimetres. Lines join teeth of one individual.

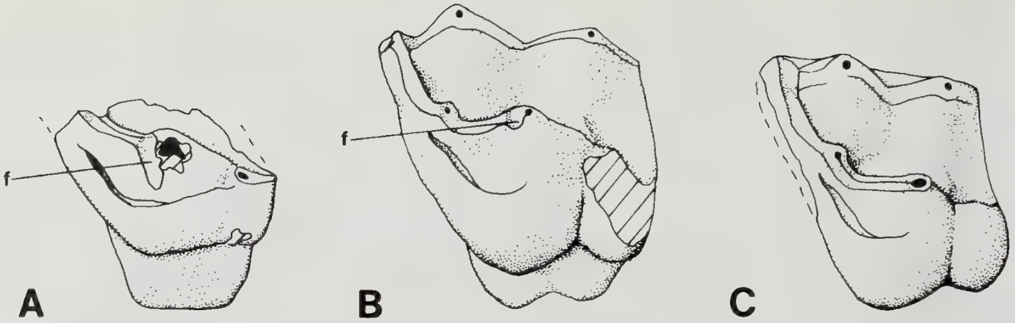
different stages in the development of the metastylid. If *L. magnus* had given rise to *L. stintoni*, one would have expected specimens with metastylid small or lacking to have been concentrated at the higher end of the size scale and those with a large metastylid at the lower end. This is not so. The plots are essentially unimodal, no specimens overlapping with *L. stintoni* (see Text-fig. 27A).

A consequence of the untenability of Gingerich's *A. magnus*→ *A. parisiensis* lineage is the reinstatement of Bartonian *A. sudrei* Gingerich 1977*a* as a potential ancestor of *A. parisiensis* but not of Bartonian ?*A. laharpei* (Pictet & Humbert 1869). *A. sudrei* poses problems for the easy distinction of *Leptadapis* and *Adapis*. Various details of the cheek teeth, size of canines and first premolars, cranial and mandibular shape and structure of the humerus and astragalus (the latter two *fide* Szalay & Delson 1979: 139) facilitate separation of *A. parisiensis* from *L. magnus* and, in the case of dental characters alone, from *L. stintoni*, *L. ruetimeyeri* and *L. priscus*. According to Gingerich (1977*a*) *A. sudrei* closely resembles *Adapis parisiensis*. Nevertheless, from his measurements of mandible depth below M_1, the jaw appears to have been shallow like *Leptadapis*. *A. laharpei* was synonymized with *A. parisiensis* by Stehlin (1912: 1236–1237) but has characteristically elongated molars with widely open trigonids and an essentially central rather than slightly lingual M_{1-2} hypoconulid. Reference to either *Adapis* or *Leptadapis* is unclear. Thus the distinction of *Leptadapis* from *Adapis* is provisionally accepted herein despite the difficulty in attributing some species.

This discussion on affinities and species content is relevant for identification of the Creechbarrow material which was first listed as *Adapis* aff. *magnus* (Hooker 1977*b*). This was based on comparison with referred material of this 'well-known species'. However, the presence of two species of *Leptadapis* of slightly different sizes makes reference back to the holotype cranium of *L. magnus* important. I was unable to find mention in the literature of its repository; moreover Cray (1973: 67) stated 'specimen not located'. It was figured by Filhol (1874, 1877*b*) and Gervais (1876), but it is not clear whether or not Stehlin saw it; he briefly mentioned it, stating that it was a relatively small individual (Stehlin 1912: 1238, 1246). Dr Marc Godinot has kindly provided me with a cast of the dentition of the specimen which is in fact in the MNHN (no. Qu.11002); measurements are shown in Text-fig. 26. According to these it is not as small as Filhol's figure (1874: pl. 8, fig. 12) would suggest. It also has a shorter M^3 than specimens which have been referred to *L. magnus*, from Hordle Cliff and Euzet (Gingerich 1977*b*: fig. 1, tab. 1). It is larger than the holotype of *L. stintoni*. A further complication is that Stehlin (1912: 1277–1280, figs 286–287) named a very small and apparently primitive individual *Adapis magnus* var. *leenhardti*, which is close to *L. stintoni* in size. Unfortunately the main primitive characters noted by Stehlin (those of canine and M^3) belong to teeth missing from the holotype of *L. stintoni*.

LOWER MOLAR METASTYLID. Stehlin (1912: 1242) noted that the metastylid was well developed on many individuals of *L. magnus* but that it could not be considered a constant character. One specimen totally lacking this cusp he considered to be an early mutation. Its presence and size in the Hordle Cliff assemblage is fairly constant for eight specimens. There also appears to be a distinct trend for increase in development of this cusp with time as Stehlin thought, e.g. it is larger in *L. stintoni* from the Upper Headon Beds than for *L. magnus* from the Lower Headon Beds and Auversian *L. ruetimeyeri* from Egerkingen α lacks it entirely.

Large size of the lower molar metastylid is associated with a greater obliquity of the protocristid than in those individuals where the metastylid is weak or missing. By placing specimens in a morphological series, it appears that as the metastylid 'grew', the metaconid migrated distolingually, resulting in a longer, more oblique tricuspid protocristid. Concomitant changes in the upper molars should have involved distal migration of the protocone leading to a more oblique preprotocrista. This possible obliquity is difficult to observe especially in isolated teeth because of variation in angle of the mesial and buccal margins of the teeth. Details of occlusion are described by Gingerich (1972). Even though the types of *L. magnus* and *L. magnus* var. *leenhardti* do not include the lower dentition, it should be possible to judge the states of development of their metastylids, by the development (or absence) of an extra buccal phase



Text-figure 28 Oblique mesiolingual views of upper preultimate molars of *Leptadapis*, in A and B showing facet (f) on protocone caused by wear against a lower molar metastylid. A, left M^2 of holotype of *L. stintoni* (Gingerich) (M32135) from the Lignite Bed, Headon Hill Limestone, Headon Hill. B, left M^1 of *L.* aff. *magnus* (M3672) from the Lower Headon Beds, Hordle Cliff. C, right M^1 (reversed) of holotype of *L. magnus* (Filhol) (MNHN Qu11002) from the Phosphorites, Raynal (drawn from cast). All × 5·3.

facet on the upper molar protocones. This concave facet was not mentioned by Gingerich (1972), but when present is situated at the lingual end of his facet B5. Its weak development in four Hordle Cliff specimens and strong development in the holotype of *L. stintoni* matches the degree of development of their respective lower molar metastylids (see Text-fig. 28A–B). Unfortunately five further Hordle Cliff specimens in similar wear states do not show this facet; moreover, none of the Creechbarrow upper molars are well enough preserved to show presence or absence of this facet. In the holotype of *L. magnus* it is absent (Text-fig. 28C). In view of its variation in the Hordle Cliff assemblage, its absence in the holotype cannot be taken as unequivocal evidence of metastylid absence too, although it is likely that this cusp was at best fairly small in this individual. Metastylid absence in the Creechbarrow assemblage, evidence for post-Bartonian acquisition of this cusp and shortness of M^3 of Qu11002 all suggest that type *L. magnus* was probably Marinesian or early Ludian in age.

Leptadapis **aff.** ***magnus*** (Filhol 1874) Gervais 1876
(Pl. 11, figs 1–6; Pl. 12; Text-figs 26–28; Table 11)

v. *1977b* *Adapis* aff. *magnus* Filhol; Hooker: 141
v. *1980* *Adapis* aff. *magnus* Filhol; Hooker & Insole: 38.

HOLOTYPE OF SPECIES. Cranium (MNHN Qu11002). Phosphorites du Quercy, Raynal, France.

DIAGNOSIS OF SPECIES. No suitable diagnosis exists because of the problems discussed above. It should await comprehensive study of all available material especially from the type area.

MATERIAL. Left P^2 (M37694), right P^3 (M35441), right P^4 (M37177), left $M^{1/2}$ (M37176), right $M^{1/2}$ (M37695), left M^3 (M37696), broken right M^3 (M37178), two left lower canines (M37179–80), two right lower canines (M35442, M35754), right P_2 (M35443), three left $M_{1/2}$s (M35444, M37181–2), right $M_{1/2}$ (M35445), right M_3 (M37183), right lower molar trigonid fragment (M37184).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. P^2 is longer than broad, oblique and has a fairly broad lingual cingular shelf, lacking protocone.

P^3 is narrow lingually with poorly-developed protocone. The parastylar area is broken away. Unlike most *L. magnus* it has a metacone, which is, however, smaller than the paracone; this is recorded by Schmidt-Kittler (1971*b*: 175, text-fig. 1) for a *Leptadapis* from Ehrenstein 1A.

Table 11 Length (l) and width (w) measurements of *Leptadapis* aff. *magnus* from Creechbarrow. Measurements in millimetres.

No.	Tooth	l	w
M37694	LP^2	5·0	4·3
M35441	RP^3	(5·0)	5·8
M37177	RP^4	5·6	(6·7)
M37176	$LM^{1/2}$	6·6	7·4
M37695	$RM^{1/2}$	5·7	7·5
M37178	RM^3	5·4	–
M37696	LM^3	5·0	7·4
M37179	LC_1	–	4·3
M37180	LC_1	–	3·6
M35754	RC_1	–	4·1
M35443	RP_2	(5·0)	–
M35444	$LM_{1/2}$	7·2	5·0
M37181	$LM_{1/2}$	7·9	5·6
M37182	$LM_{1/2}$	7·0	5·0
M35445	$RM_{1/2}$	8·0	5·3
M37183	RM_3	(8·5)	(4·1)

P^4 is also typical for *L. magnus* in its length/width proportions and in having a well-developed metacone. *L. ruetimeyeri* has a much shorter P^4 (see Stehlin 1916: pl. 21, figs 27, 29–30).

The $M^{1/2}$s available are not well preserved but appear to be relatively slightly shorter than in *L. magnus*, thus rather more like those of *L. ruetimeyeri* (see Text-fig. 26; Pl. 11, fig. 4; and Stehlin 1916: pl. 21, figs 22–23, 27, 29, 31).

M^3 is also relatively short like most *L. ruetimeyeri* (see Text-fig. 26; Pl. 11, fig. 5; and Stehlin 1916: pl. 21, figs 28, 31). Stehlin (1916: pl. 21, fig. 5) showed an *L. ruetimeyeri* M^3 which is more like *L. magnus* in proportions. This tooth tends to be variable as it is the last in the row but its shortness in the Creechbarrow *Leptadapis* can be considered primitive compared with Ludian assemblages. A reduced M^3 in '*A.*' *magnus* var. *leenhardti* led Stehlin (1912: 1278) to consider this variety to be primitive and to be of Bartonian age; it is much smaller than the Creechbarrow *Leptadapis*.

M37180 (Pl. 11, fig. 6), the best preserved lower canine, is unlike the other three as well as those of *L. magnus* from various localities and that of *L. ruetimeyeri* in lacking a lingual cingulum. In two specimens from the Phosphorites du Quercy the distolingual and distobuccal crests extend separately right to the apex of the tooth, whereas on M37180 and (according to Stehlin's 1912: 1268, text-fig. 282 of NMB Ef972) *L. ruetimeyeri*, these crests die out about two-thirds of the distance towards the apex, whereupon they are replaced by a median distal crest which tops the apex. This appears to be another primitive feature of the Creechbarrow assemblage, but the character may be variable.

P_2 is broken distolingually and shows few features of interest except a high buccal cingulum.

The four $M_{1/2}$s fall into two size groups, two specimens plotting within the range of Hordle Cliff M_1s, two more plotting within the range of Hordle Cliff M_2s (Text-fig. 27A). They are tentatively distinguished likewise since their morphologies are identical. All the Creechbarrow specimens have a strong postmetacristid but no development of a metastylid in this region. The Hordle Cliff assemblage has quite a constant weak development of this cusp. Stehlin (1912: 1242) considered absence of this cusp in *L. magnus* to represent an early mutation. This idea is thus confirmed and its dating is shown to be Marinesian.

On M_3 the postmetacristid is less stongly developed than on $M_{1/2}$ but more so than on *L. ruetimeyeri* M_3. There is no entoconid.

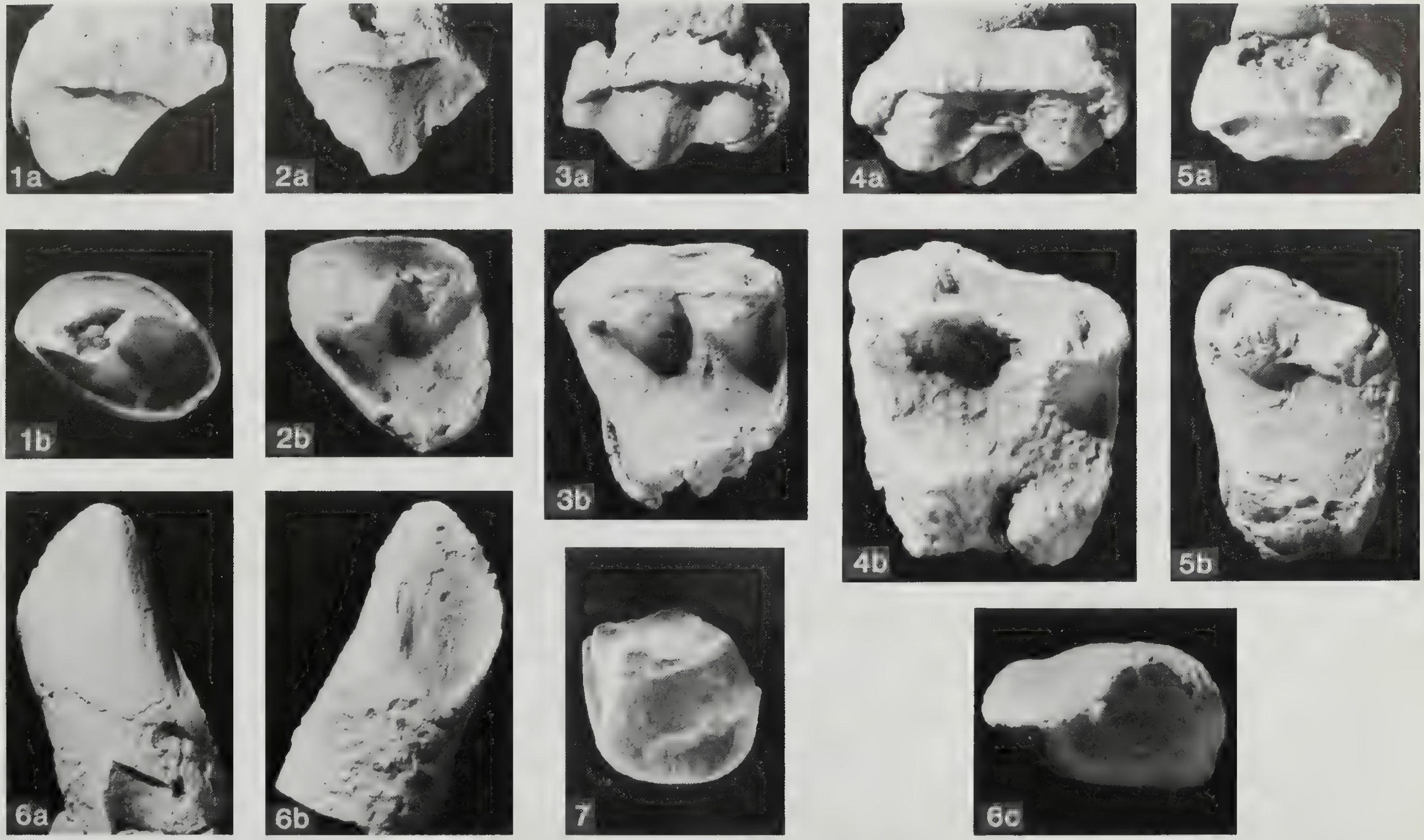


Plate 11 Teeth of Adapinae from Creechbarrow.

Figs 1–6 *Leptadapis* aff. *magnus* (Filhol). Light macrographs of upper cheek teeth and lower canine, × 6. a, buccal, b, occlusal and c, lingual views. Fig. 1a, b, left P^2 (M37694). Fig. 2a, b, right P^3 (reversed) (M35441). Fig. 3a, b, right P^4 (reversed) (M37177). Fig. 4a, b, left $M^{1/2}$ (M37176). Fig. 5a, b, left M^3 (M37696). Fig. 6a–c, left lower canine (M37180). See p. 278.

Fig. 7 Adapinae indet. Scanning electron micrograph, × 12. Lingual half of right $M^{1/2}$ (reversed) (M37692). See p. 282.

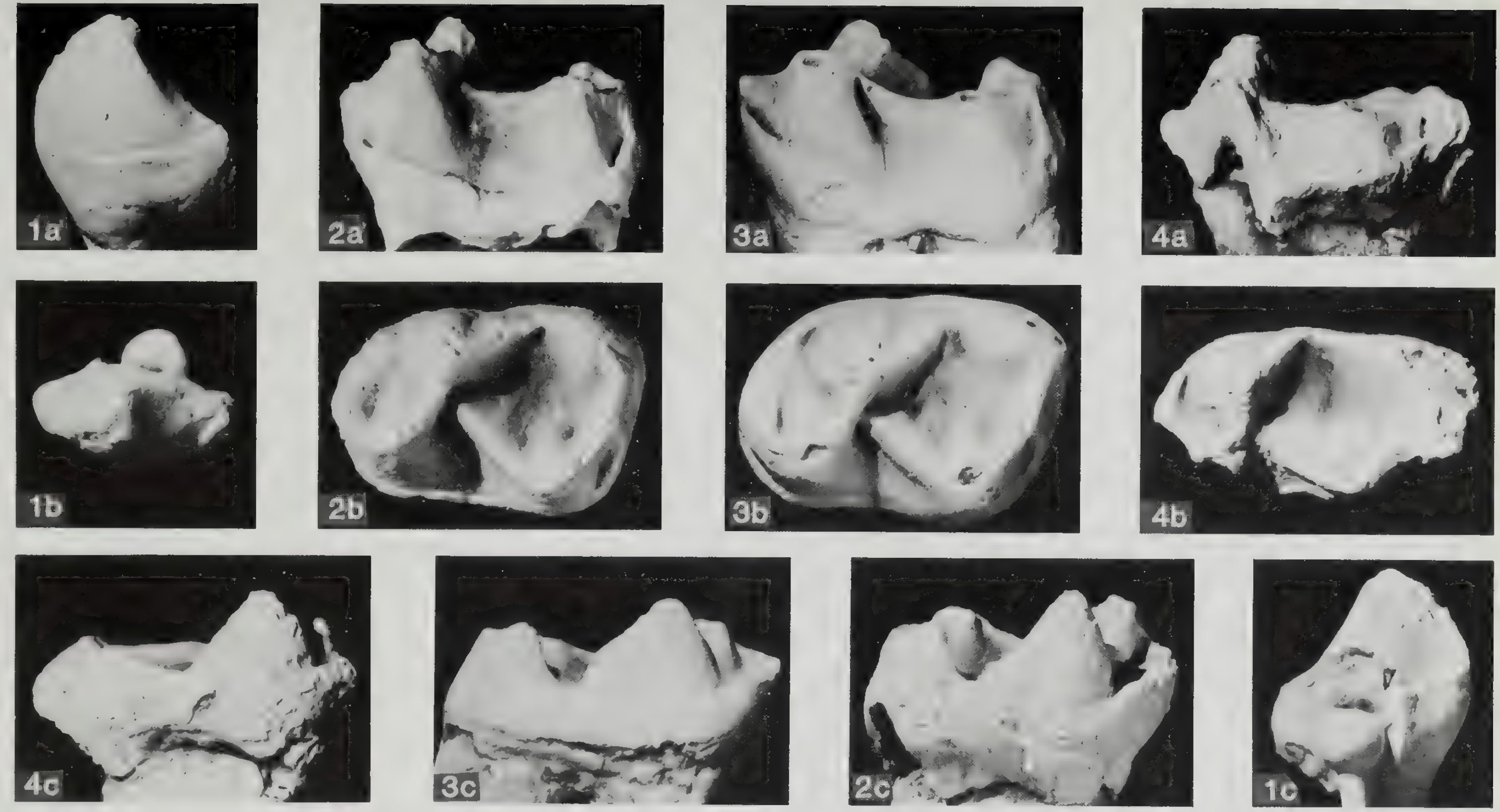


Plate 12 Light macrographs of lower cheek teeth of *Leptadapis* aff. *magnus* (Filhol) from Creechbarrow, × 6. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, right P_2 (reversed) (M35443). Fig. 2a–c, left $M_{1/2}$ (M35444). Fig. 3a–c, left $M_{1/2}$ (M37181). Fig. 4a–c, right M_3 (reversed) (M37183). See p. 278.

Thus the Creechbarrow *Leptadapis* in a variety of characters is more primitive than the referred assemblages of *L. magnus* from stratified deposits, which hitherto have all been post-Bartonian in age. In size of lower molars and width of uppers it is closer to *L. magnus* than to the small *L. stintoni* or '*L. magnus* var. *leenhardti*'. If the last should be Bartonian too, then the two lineages of *Leptadapis* must have already been established by the Marinesian. Auversian *L. ruetimeyeri* is then the best candidate for their common ancestry, giving rise to each by slight increase and decrease in size along with the relevant grade changes. The choice of name for the Creechbarrow assemblage is an attempt at conservatism, indicating probable lack of total identity with typical *L. magnus* and awaiting more material and solutions to the problems posed by the mixed faunas of the old Phosphorites collections.

Adapinae, gen. et sp. indet.
(Pl. 11, fig. 7)

MATERIAL. Lingual half of right $M^{1/2}$ (M37692).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. This tooth fragment is indeterminate generically but is of interest as indicating the presence of a third adapine in the Creechbarrow fauna. Its length is estimated at 2·35 mm. It has a strong lingual cingulum on which is developed a small hypocone. The valley bottom between the protocone and hypocone is bridged by a very faint crest. The postprotocrista is directed distally and only slightly buccally from the protocone and only the very beginning of its bend to a buccal direction is preserved.

Its greatest similarity is with *Periconodon* but it differs in lacking a pericone completely and in the hypocone having a lesser lingual extent. These features do, however, appear to be variable in extent in the type species (cf. Stehlin 1916: pl. 22, fig. 3 with fig. 11; and see discussion by Gingerich 1977*a*: 70–71). In size it is very close. It cannot be excluded that it might be an M^2 of *Microadapis*, although here the paraconule and metaconule are prominent and the hypocone probably ought to be larger (only M^1 is known of the upper dentition of *Microadapis*).

If more material should be found supporting reference to either genus, it would mean an upward extension of stratigraphical range from the late Lutetian.

Order **RODENTIA** Bowdich 1821

Suborder **SCIUROGNATHI** Tullberg 1899

Infraorder **PROTROGOMORPHA** Zittel 1893

Family **PARAMYIDAE** Miller & Gidley 1918

One of the two named genera concerned here (*Plesiarctomys*) was placed in the Ischyromyidae, subfamily Paramyinae in Simpson's (1945) classification. Wood (1962) in a major review raised the Paramyinae to family status and the tribe Manitshini (Simpson 1941) to subfamily status, including *Plesiarctomys* in it. He also included *Ailuravus* (another genus occurring in the English Bartonian) in the Paramyidae, but *incertae sedis*. Michaux created the paramyid subfamilies Ailuravinae Michaux 1968 for *Ailuravus* and its probable ancestor *Meldimys* Michaux 1964; and Pseudoparamyinae Michaux 1964 for *Plesiarctomys* and its probable ancestor *Pseudoparamys* Michaux 1964. His two reasons for separating *Plesiarctomys* from the Manitshinae (1968: 154) were that *Plesiarctomys* represented a lineage separate from the large North American manitshines, and was derived probably from *Pseudoparamys*; and that manitshines the same age as *Pseudoparamys* were already large and thus the 'rhythm' of the *Plesiarctomys* group was different. There appears on the contrary to be little except size to prevent *Pseudoparamys* from being included also in the Manitshinae. Hartenberger (1975: 779) included the Pseudoparamyinae in the Paramyinae and considered that the grouping of *Plesiarctomys* with the North American manitshines was artificial and only founded on convergent features, but did not give details. One cannot necessarily assume that the dental features that link the manitshines and *Plesiarctomys* are due purely to large size, since *Ailuravus*, another distinct European paramyid genus, is approximately the same size as *Plesiarctomys* but morphologically very different.

A higher taxonomic change occurred when Black (1968) showed that *Ischyromys* Leidy 1856 was scarcely more advanced in lophodonty of the cheek teeth (Wood's 1962 reason for separating it and *Titanotheriomys* Matthew 1910 in the Ischyromyidae from the Paramyidae) than are the paramyids and was closely related to them. He therefore assimilated the two families, Ischyromyidae being the prior name. He was followed by Black (1971) and Hartenberger (1975). Wood (1970) and Bosma (1974) followed Wood (1962) in placing *Plesiarctomys* in the manitshine paramyids. Wahlert (1974), in a study of the cranial foramina of protrogomorphs, concluded that *Ischyromys* was not closely related to the other genera that Black (1968) had included in the Ischyromyidae and reinstated the family Paramyidae to accommodate them. He was followed by Wood (1976*a*). Wood (1976*b*) further supported the separation of Paramyidae and Ischyromyidae on other cranial and dental evidence and (1980: 17–19) gave a full review of the dispute. Wahlert's (1974) and Wood's (1976*b*, 1980) conclusions are followed here. *Plesiarctomys* is included in the Manitshinae for strong morphological reasons and *Ailuravus* in the Ailuravinae.

Subfamily **MANITSHINAE** Simpson 1941

Genus ***PLESIARCTOMYS*** Bravard 1850

Type species. *P. gervaisii* Bravard 1850. Ludian, La Débruge, France.

Included species. *P. savagei* (Michaux 1968) Hartenberger 1975, *P. hartenbergeri* Wood 1970, *P. spectabilis* (Major 1873) Stehlin & Schaub 1951, *P. hurzeleri* Wood 1970 and *P. curranti* sp. nov.

Range. Late Ypresian to Ludian, England, France, Switzerland and ?Spain.

Diagnosis (as emended by Wood, 1970). 'Medium to large sized manitshine; cresting of cheek teeth developing progressively within the genus, and more prominent than in any other manitshine except *Manitsha*; cusps of lower teeth swelling into talonid basin and reducing size of lingual gorge; P_4 small; third upper premolar progressively lost; frequently a junction of mesostyle and posterior cingulum lateral to metacone especially in P^4 and M^1; pulp cavity of incisors tending to be constricted from the sides'.

Note. Wood (1970) has made a thorough review of this genus and should be consulted for the early synonymies, history of investigations, comprehensive descriptions and figures of most aspects of the known species except *P. savagei*. The dental nomenclature diagram (Text-fig. 31) will suffice for most aspects of *Plesiarctomys* teeth.

Plesiarctomys curranti sp. nov.

(Pl. 13, figs 1–8; Text-figs 29, 30A)

v. *1977b* *Plesiarctomys* sp. 2; Hooker: 141.
v. *1980* *Plesiarctomys* sp. 2; Hooker & Insole: 39.

Name. After Mr A. P. Currant, for help with field work.

Holotype. Right M_1, M37188. Pl. 13, fig. 6.

Paratypes. (9): Left $M^{1/2}$ (M35446), right $M^{1/2}$ (M35447), left M^3 (M37702), two right M^3s (M35448, M35763), left DP_4 (M35764), right P_4 (M35765), right M_2 (M35450), left M_3 (M35449).

Type horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Small *Plesiarctomys*, length of $M_1 = 3{\cdot}3$ mm. Upper and lower molars with distantly spaced buccal and lingual cusp tips, leaving broad intervening basins in which the enamel is nearly always finely wrinkled. Height of talonid basin above crown base in M_1 less than one-third of length of tooth. M_{1-2} hypolophulid absent. Lower molar sinusid broad and ectolophid complete; M^{1-2} endoloph with very shallow to absent lingual groove separating protocone from hypocone. [Mandible unknown. Incisors not definitely known].

DIFFERENTIAL DIAGNOSIS. *P. savagei* is poorly known but has an incomplete $M_{1/2}$ ectolophid.

P. spectabilis and *P. hartenbergeri* are much higher crowned; their unworn buccal and lingual cusp tips are closer together; their enamel is much more coarsely wrinkled, often in a radiating pattern; lingual groove separating M^{1-2} protocone and hypocone present.

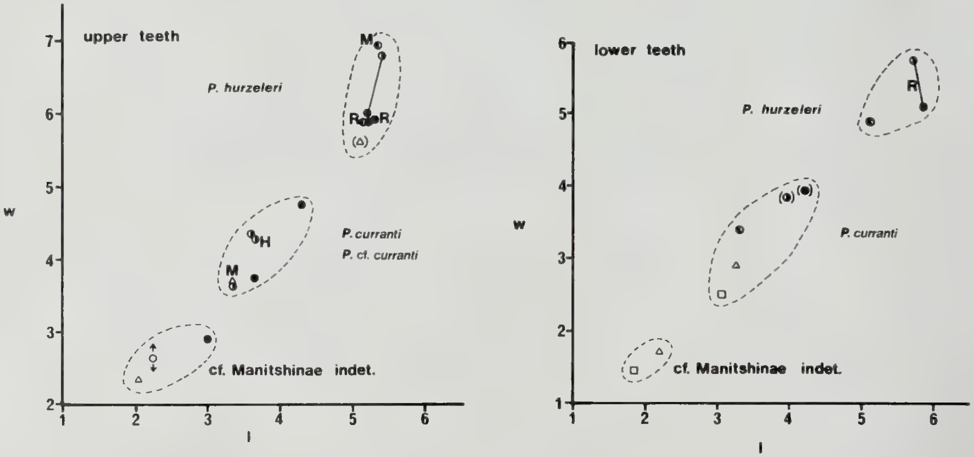
P. hurzeleri and *P. gervaisii* are larger and have partial to complete M_{1-2} hypolophulid. Enamel wrinkling replaced by a few coarse lophules in the basins. Crown height and spacing of cusps intermediate between *P. curranti* and *P. spectabilis.*

DESCRIPTION. No upper permanent or deciduous premolars have been found. The possibility of a P^4 from Mormont belonging to this species is discussed below.

$M^{1/2}$: Wood (1970: 247) distinguished between isolated M^1s and M^2s on the buccal extent of the posteroloph: i.e. in M^1 it extends buccal to the metacone, sometimes even joining the mesostyle, whereas in M^2 it stops distal to the metacone which then forms the buccal margin at this point on the tooth. On this criterion, both M35446 and M35447 are M^2s. The latter is larger than the former and its lesser proportional length is likely to be due to considerable natural wear which has removed the mesial and distal flared margins of the tooth (Pl. 13, figs 1–2).

M35446 has a prominent mesostyle but short weak mesoloph, a hypostyle is differentiated on the posteroloph and the moderate wear has only removed some of the finely granular enamel wrinkling of the trigon basin.

M35447, although considerably more worn than M35446, shows a small mesostyle detached from a somewhat longer, more prominent mesoloph; the posteroloph appears to bear no hypostyle but is joined to the metaloph by a posterolophule. Enamel wrinkling is not obvious but may have been removed by wear.



Text-figure 29 Scatter diagrams of length (l) against width (w) in upper and lower cheek teeth of *Plesiarctomys hurzeleri* Wood, *P. curranti* sp. nov., *P.* cf. *curranti* and cf. Manitshinae indet. (p. 290). □ = DP4; △ = P4; ◐ = M1; ◑ = M2; ○ = M1/2; ● = M3. Initial letters indicate that the specimens come from Mormont (M), Robiac (R) and Headon Hill 1 (H). The rest come from Creechbarrow. Measurements in millimetres.

Both teeth in mesial or distal view show a near vertical orientation of the lingual cusps relative to the plane of the crown base. This can be strongly contrasted to the very sloping orientation associated with a greater lingual crown height in *P. spectabilis* (see Text-fig. 30A–B, and Wood, 1970: 262, fig. 10A). This was referred to by Wood (1970: 246) as 'rather striking unilateral hypsodonty' and considered a generic feature, but it is less marked in *P. hurzeleri* and *P. gervaisii* and less marked still in *P. curranti*. Another feature of both M35446 and M35447 is the short buccal cingulum extending from the parastyle part way round the paracone.

M^3: Of the three M^3s only M37702 is well enough preserved to show detailed features (Pl. 13, fig. 3). M35448 is very worn and M35763 is corroded, particularly round the crown base. M37702 is large compared with the other upper molars and has rather coarse enamel wrinkling like *P. spectabilis* or *P. hartenbergeri*. The protocone has the lingual slope typical of *P. spectabilis* but lower height than in the preultimate molars of this species. M^3, however, tends to be a non-distinctive tooth, not showing the specializations often seen in M^{1-2}.

DP_4 : M35764 is poorly preserved but was originally probably only slightly worn and shows the distinctive fine enamel wrinkling in the talonid basin. The complete ectolophid and high length/distal width ratio identify it as a DP_4 (Pl. 13, fig. 4). Otherwise it has few distinctive features.

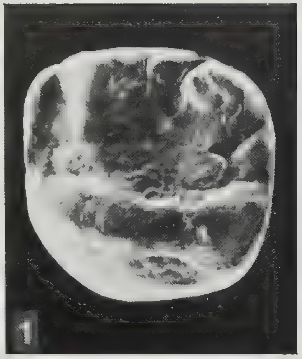
P_4: Wood (1970: 247) stated that in *Plesiarctomys* 'the trigonid is narrow ... and the protoconid usually looks merely like a basal cingulum on the metaconid. As a result the trigonid basin is minute.' M35765 has the protoconid broken away but is much broader in the region of the trigonid than in most other *Plesiarctomys* P_4s, although the protoconid is still likely to have been a small cusp (Pl. 13, fig. 5). Another peculiarity is that the sinusid is completely filled by a greatly enlarged ectostylid. There appears to have been no hypolophulid. As stated above, a high length/distal width ratio is typical of DP_4 whereas in P_4s the ratio is 1 : 1. In M35765 it is greater than 1 : 1, but the tooth can be confirmed as a P_4 because its enamel is significantly thicker than that of M35764 and the same thickness as that of the molars.

M_1: M37188 has no hypoconulid developed on the posterolophid, which is continuous but shows slight constrictions as it approaches both entoconid and hypoconid. When unworn there would probably have been interruptions. The sinusid is deep distally and there is a small but distinct mesoconid but no sign of a hypolophulid. The ectolophid is essentially complete but thin distal to the mesoconid and fissured immediately mesial to the mesoconid. The fine enamel wrinkling remains after moderate wear. The mesially tapering outline is distinctive of M_1 (Pl. 13, fig. 6).

M_2: M35450 is corroded but only slightly naturally worn (Pl. 13, fig. 7). The fine enamel wrinkling tends to be reticulate rather than granular but this may partly be due to the surface corrosion. Its outline is typically rectangular and the posterolophid, although partly broken away, appears to have been interrupted and without a hypoconulid. A small lophule extends lingually a short distance from the ectolophid but is not sufficiently distinct to deserve the term partial hypolophulid. The ectolophid is low but complete and the mesoconid is very weakly represented. The sinusid is deep distally as on M37188.

M_3: M35449 is broken at the buccal and distal edges of the crown, but is identified as M_3 because it appears to show more distal expansion than either M35450 or M37188. The tooth is hardly worn and the fine enamel wrinkling is well preserved, showing it to be partly granular, partly reticulate in pattern (Pl. 13, fig. 8). A complete hypolophulid runs from the low entoconid to the ectolophid near its distal end. It bears three small, equally spaced cuspules. The ectolophid is divided into two parts with an intervening low area, not a fissure. There is slight but not distinct formation of a mesoconid on the buccal wall of the distal half. The sinusid is deep distally. There is a deep pit towards the buccal side of the talonid basin which may be pathological.

These descriptions probably refer mainly to individual states, there being too few specimens to judge intraspecific morphological or size variation. Nevertheless, I have tried to use in the diagnosis those features shown by Wood (1970) to show the least variation in better represented species of *Plesiarctomys* and which appear to have a particular constancy within the specimens described here.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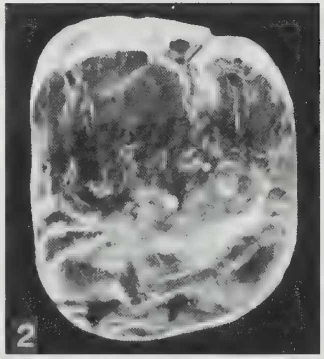
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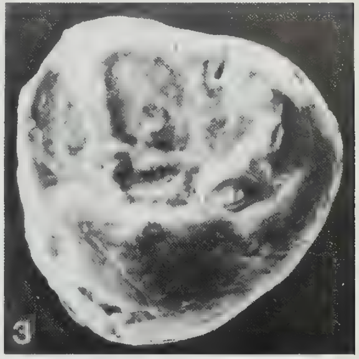
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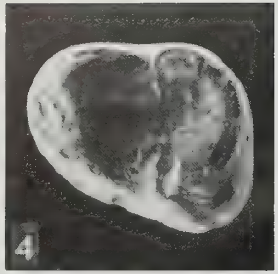
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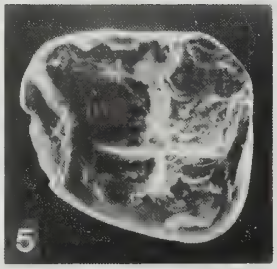
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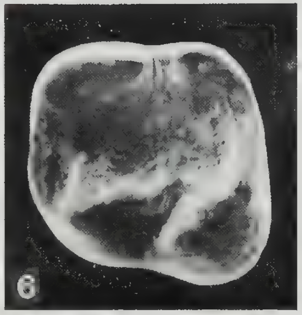
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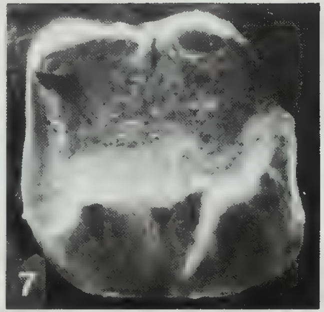
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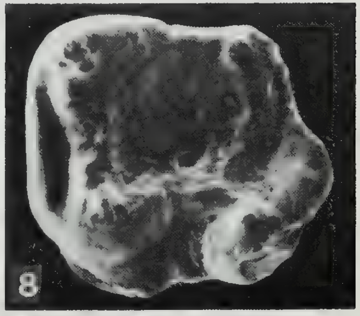
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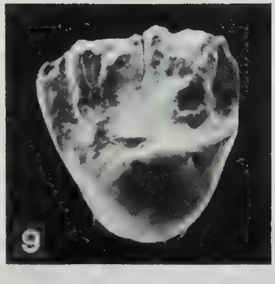
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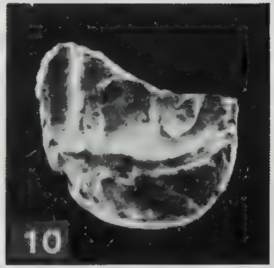
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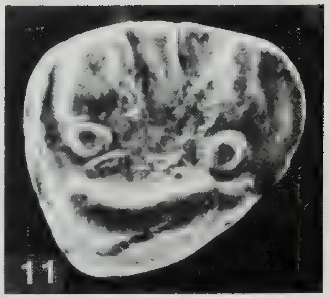
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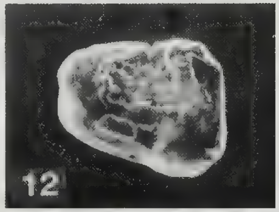
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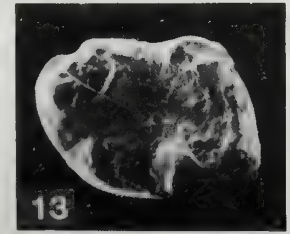
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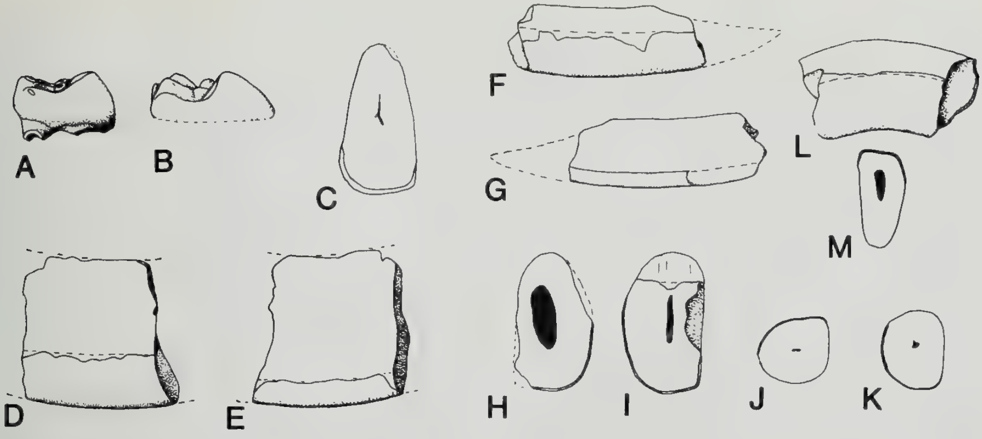


Text-figure 30 A, mesial view of left $M^{1/2}$ (M^2?) of *Plesiarctomys curranti* sp. nov. (M35446). B, mesial view of right M^2 (reversed) of *Plesiarctomys hartenbergeri* Wood (UM Bw56-17), drawn from cast. C–E, lower incisor fragment of ?*Plesiarctomys* sp. (M35451). C, transverse section; D, distal view; E, mesial view. F–I, lower right incisor of Rodentia indet. (M37190). F, distal view; G, mesial view; H, basal transverse section; I, occlusal transverse section. J–K, transverse sections of incisors of *Ailuravus stehlinschaubi* Wood. J, left upper incisor (M35698); K, right lower incisor (M37198). L–M, upper incisor fragment of Rodentia indet. (probably *Sciuroides rissonei* sp. nov. (M37391). L, distal view; M, transverse section. A–G, J–M are × 4; H–I are × 8. B is from the marnes vertes, Bouxwiller; the rest are from the Creechbarrow Limestone Formation, Creechbarrow. In the transverse sections, enamel is shown by a double line in C, H and I; and by a single thickened line in J, K and M.

One important feature is crown height, but because the cusps of *Plesiarctomys* teeth are so often worn, this is difficult to measure. It can, however, be judged by the height of the base of the talonid basin above the crown base. In *P. spectabilis* there appears to be a gradient of crown height increasing from M_3 to M_1, so that $M\frac{1}{1}$ is the best tooth in the row from which to estimate crown height differences between the species. It is partly for this reason that M_1 is chosen as the holotype of *P. curranti*.

Discussion. There are two teeth from other localities which may have affinities with *P. curranti*. The first is an M^2 from the lower part of the Lower Headon Beds of Headon Hill (HH1), Isle of Wight, described and figured by Bosma (1974: 97, pl. 4, fig. 10). It is broadly similar to the two M^2s(?) from Creechbarrow; i.e. it is similar in size and has near vertical lingual cusps which are widely spaced from the buccal cusps. It lacks, however, the short buccal cingulum on the paracone. This may not be a diagnostic character of *P. curranti* but it is not evident in any of Wood's (1970) figures of *Plesiarctomys*.

The second tooth is LGM LM 2936, a right P^4 from Mormont, Switzerland. It is distinctly more molariform than those of *P. spectabilis*, *P. hartenbergeri*, *P. savagei* or *P. hurzeleri* (P^4

Plate 13 Scanning electron micrographs of occlusal views of paramyid cheek teeth from Creechbarrow.

Figs 1–8 *Plesiarctomys curranti* sp. nov., × 10. Fig. 1, left $M^{1/2}$ (M^2?) (M35446). Fig. 2, right $M^{1/2}$ (M^2?) (reversed) (M35447). Fig. 3, left M^3 (M37702). Fig. 4, left DP_4 (M35764). Fig. 5, right P_4 (reversed) (M35765). Fig. 6, **holotype** right M_1 (reversed) (M37188). Fig. 7, right M_2 (reversed) (M35450). Fig. 8, left M_3 (M35449). See p. 283.

Figs 9–13 ?Manitshinae indet., × 12·5. Fig. 9, right P^4 (reversed) (M35452). Fig. 10, right $M^{1/2}$ (reversed) (M35767). Fig. 11, left M^3 (M35536). Fig. 12, right DP_4 (reversed) (M35768). Fig. 13, right P_4 (reversed) (M37189). See p. 290.

unknown in *P. gervaisii* but P_4 is like the other previously-described species). It also differs in being nearly as long as wide and with more widely spaced paracone and metacone; it has an incipient hypocone which is not divided from the protocone by a lingual groove on the endoloph. There is moderately fine granular enamel wrinkling. The posteroloph continues part way round the metacone buccally. The paracone and metacone are joined on the buccal edge by a ridge which is papillate but not distinctly differentiated into a mesostyle. There is a small interstitial facet, just lingual to the parastyle, indicating the former presence of P^3 or retained DP^3 (see discussion on the presence of these teeth in *Plesiarctomys* by Wood, 1970: 244–246). The suggestion that this tooth might be conspecific with *P. curranti* is based on the morphology of P_4 of this species. Its greater proportional length and consequent spacing of protoconid and hypoconid could possibly provide a pattern which could suitably occlude with the Mormont P^4. The problem can only be solved, however, by finding corresponding teeth at either Creechbarrow or Mormont. There is no information on the label with the Lausanne Museum specimen as to whether it came from Eclépens-Gare or Entreroches.

Two lower incisor fragments from Creechbarrow (M35451, M35766) too large to belong to any of the pseudosciurids known by their cheek teeth at this locality are potential candidates for attribution to the present species. The more complete (M35451) is slightly narrower than the species with the narrowest lower incisors (*P. hartenbergeri*) (Text-fig. 30C–E). In fact the proportions are more that of a pseudosciurid. If the incisor should really belong to *P. curranti*, its length/width proportions would be a further diagnostic character. In the broken section of the dentine, it is just possible to see a triangular, laterally pinched pulp cavity typical of *Plesiarctomys*.

Plesiarctomys hurzeleri Wood 1970

(Pl. 14, figs 1–3; Text-fig. 29)

vp. 1873 *Sciuroides* sp.; Major: pl. 3, fig. 7.
v* 1970 *Plesiarctomys hurzeleri* Wood: 255–257, figs 5–6.
v. *1977b* *Plesiarctomys* sp. 1; Hooker: 141.
v. *1980* *Plesiarctomys* sp. 1; Hooker & Insole: 39.

HOLOTYPE. Left mandibular ramus with M_{1-2} (FSL 4912). Lower Calcaire de Fons, Robiac, Gard, France.

RANGE. Marinesian, Creechbarrow, England; Robiac and La Millette, France (Wood's 1970 discrediting of the last record arose from his confusion between Castres and Castrais, localities of different ages). Also from the fissure deposits of Mormont, Switzerland, and Quercy, France.

MATERIAL. Left P^4 (M35761); right M^{2-3} (M37185); left M^3 (M37186) (possibly the same individual as M37185); left M_1 (M37187); and a fragment of left $M_{1/2}$ (M35762).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS. Medium-sized *Plesiarctomys*, length of $M_2 = 5{\cdot}38$ mm. Upper and lower molars with moderately spaced buccal and lingual cusp tips, with shallow intervening basins with a few coarse lophules and no enamel wrinkling. Height of talonid basin above crown base in M_1 about half the length of the tooth. M_{1-2} hypolophulid nearly continuous. Lower molar sinusid narrow and ectolophid complete. M^{1-2} endoloph with very shallow to absent lingual groove separating protocone from hypocone. Anterior margin of pterygoid fossa of mandible vertical. Upper incisors nearly as long (mesiodistally) as wide (buccolingually), with one or two faint sulci.

REASONS FOR EMENDATIONS. Characters here removed from Wood's (1970) diagnosis are those which I consider are subject to individual variation and had originally been included because no more than one specimen of any cheek tooth type was then known.

1. The apparent absence of two hypoconulids from the Creechbarrow M_1 and the variation of this character in *P. gervaisii* (Wood 1970: 253, figs 4A–C) make it unsuitable as a specific character.

2. The presence of only three roots (one mesial, two distal) instead of four in the Creechbarrow M_1 and some variation in their number in *P. spectabilis* (Wood 1970: 265) requires emendation of this character. For *P. gervaisii*, Wood (1970: 249) stated 'lower molars with three or, rarely, four roots apiece', but (1970: 254) 'All of the lower molars preserved have three roots'. In view of the other close similarities of the Creechbarrow M_1 to the holotype of *P. hurzeleri*, it seems best to consider these as conspecific and the root number as slightly variable.

3. Variation in size of M^1 hypocone in *P. gervaisii* (Wood 1970: 251, figs 2A, C, D) suggests that a similar degree of difference between the Creechbarrow and Robiac upper preultimate molars is not of specific value.

4. Other modifications are to make the diagnosis compare feature for feature with *P. curranti*.

Differential diagnosis. *P. savagei* is smaller and has an incomplete $M_{1/2}$ ectolophid.

P. spectabilis and *P. hartenbergeri* are smaller and higher-crowned; their unworn buccal and lingual cusp tips are closer together; their enamel is coarsely wrinkled, often in a radiating pattern; a lingual groove separating M^{1-2} protocone and hypocone is present; they have one mesial and one distal lower molar root; their incisors lack sulci; and *P. hartenbergeri* incisors are also relatively shorter.

P. gervaisii is slightly larger and has two mesial and one distal lower molar roots.

P. curranti is smaller and lower-crowned; its unworn buccal and lingual cusp tips are further apart; its enamel is finely wrinkled; its lower molar sinusid is broader.

Description. P^4: This tooth is badly corroded but is important as being the first upper premolar to be attributed to this species (Pl. 14, fig. 1). This is based on size and the steeper slope of the lingual wall compared to *P. spectabilis*. From Wood's (1970) figures, the outline of *P. spectabilis* P^4 varies considerably and M35761 does not differ significantly except that the parastyle is more prominent, thus increasing the length/width ratio. A small hypocone is weakly differentiated from the protocone on the postprotocingulum. The paraconule is buccal to the midline and the paracone and metacone appear small and joined by a strong buccal cingulum with no sign of a mesostyle or mesoloph. However, bad preservation makes clear recognition of cusps and crests difficult. The tooth is less square and less molarized than LM 2936 from Mormont described under *P. curranti* (p. 287).

M^2: Almost square in outline (Pl. 14, fig. 2) in contrast to the triangular right $M^{1/2}$ (FSL 4916) from Robiac (Wood 1970: 256, fig. 6A), but very similar to the right $M^{1/2}$ from Mormont (LGM 40463: LM 2935) (figured by Major, 1873: pl. 3, fig. 7 as *Sciuroides* sp.). In both the Creechbarrow and Mormont specimens, the hypocone is larger than in FSL 4916 and there is a strong mesoloph stemming from a weak mesostyle. Unfortunately both teeth are considerably worn, obscuring most of the detail.

M^3: The suggestion that M37185 and M37186 belong to the same individual is based on near identity of wear and morphology of the M^3s and matching interstitial facets of right M^2 and M^3, supported by similar wear and preservation (Pl. 14, fig. 2). All three teeth came from the same excavation hole. The outline of the two M^3s from Creechbarrow tapers more rapidly than in the right M^3 (FSL 4917) from Robiac, which is trapezoidal, having a lingually more salient hypocone. There is some evidence of a mesoloph, lacking on FSL 4917. That specimen has a gap between the mesostyle and metacone, whereas the Creechbarrow M^3s have a continuous buccal cingulum. Other potential features have been removed by wear.

M_1: M37187 is identified as an M_1 rather than an M_2 because the outline has a slight mesial taper (Pl. 14, fig. 3). It otherwise differs from the M_2 of the holotype (Wood 1970: 255, fig. 5A) in having a wider sinusid; no obvious differentiation of the posterolophid into two hypoconulids; the hypolophulid joining the mesoconid instead of the hypoconid; a stronger ectolophid; and a single mesial root pinched in the middle. More specimens of lower molars are required before the exact degree of variation in root number can be assessed.

The left $M_{1/2}$ (M35762) is broken and corroded but shows a strong ectolophid and the hypolophulid joining the mesoconid as in M37187.

DISCUSSION. *P. hurzeleri* appears to be very closely related to *P. gervaisii* from which it differs mainly in slightly smaller size. It could stand as a good morphological ancestor for *P. gervaisii*, whose type horizon is higher (late Ludian). That *P. gervaisii* may have already evolved by the earliest Ludian is suggested by the presence at Eclépens of a P_4 (NMB Mt.1468), mentioned by Wood (1970). This locality contains fissures of both Marinesian (Eclépens-Gare and Eclépens A) and earliest Ludian (Eclépens B) age (see correlation section, pp. 422–429). The *P. hurzeleri* $M^{1/2}$ (LGM 40463: LM 2935) from Mormont unfortunately lacks more detailed locality data.

?**Manitshinae**, gen. et sp. indet.

(Pl. 13, figs 9–13; Text-fig. 29)

v. *1980 Plesiarctomys* sp. 3; Hooker & Insole: 39.

MATERIAL. Right P^4 (M35452); broken right $M^{1/2}$ (M35767); left M^3 (M35536); right DP_4 (M35768); right P_4 (M37189).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. The specific association of these teeth is by no means certain. They are smaller than any known species of *Plesiarctomys* except perhaps the unnamed upper premolar from the Lutetian of Montllobar, Spain, described by Wood (1970: 271). Apart from size, the upper teeth share prominent isolated or near isolated paraconules and metaconules and the lack of the typically inflated robust appearance of *Plesiarctomys* teeth. Their morphology is approached only slightly by the low-crowned, basined teeth of *Plesiarctomys curranti*. The anteroloph, endoloph and posteroloph form a single three quarters encircling loph on which protocone and hypocone can hardly be individually recognized.

P^4: This tooth lacks the buccal wall and is triangular in outline (Pl. 13, fig. 9). Large paraconule and metaconule arise from narrow preprotocrista and postprotocrista respectively. The metaconule is more isolated than the paraconule. The anteroloph broadens buccally towards a parastyle which is mainly broken away. A fissure separates paracone and metacone. The posteroloph bulges slightly distolingually but there is no sign of a hypocone.

$M^{1/2}$: A large buccal part of this tooth is missing (Pl. 13, fig. 10). It is considered to be a right because the more isolated of the two intermediate conules by comparison with P^4 appears to be the metaconule; and also because the more prominent of the two lingual cusps is probably the protocone.

M^3: This well-preserved tooth, unlike the previous two, is scarcely worn (Pl. 13, fig. 11). Its outline is a right-angled triangle with the distolingual edge as the hypotenuse and the mesial edge the shortest side. The metacone is only slightly smaller than the paracone and the metaconule is larger than the paraconule. There is no hypocone and the prominent posteroloph bulges distally and meets the metacone buccally. There is a prominent mesostyle terminating a strong mesoloph which extends one third the distance across the trigon basin. Distal to the main mesostyle is a fissure and then a small accessory mesostyle joined to the metacone. The enamel is finely wrinkled and two slightly coarser folds occur buccal and lingual of the paraconule. Protocristae are lacking except for a slight development between the metaconule and protocone; and the paraconule and metaconule would have remained distinct even after heavy wear. The anteroloph is weak and forms only a narrow shelf in front of the paracone.

DP_4: This tooth is corroded and enamel is missing from its buccal wall, but it shows finely wrinkled enamel in the talonid basin (Pl. 13, fig. 12). It is identified as a DP_4 by analogy with the high length/width ratio of this tooth compared to P_4 in *Plesiarctomys*. There appears to be a nearly complete hypolophulid joining the hypoconid as can occur in *Plesiarctomys* (see Wood 1970: fig. 12K). The large mesial cusp probably combines both protoconid and metaconid and there is no cingulum mesial to this.

P_4: This tooth is also corroded and distobuccally broken (Pl. 13, fig. 13). It has a distinct protoconid which is slightly smaller than the metaconid, as in *Plesiarctomys curranti*. There is a deep talonid notch, no hypolophulid and the talonid basin enamel is finely wrinkled.

Discussion. This small assemblage probably belongs to an undescribed genus. Despite some similarities, it does not fit the diagnosis of *Plesiarctomys*. There are some striking similarities to the 'genre indéterminé B' from the early Eocene of Avenay and Condé-en-Brie, France, of Michaux (1968: pl. 10, figs 7–9). The large isolated intermediate conules, strong encircling lingual loph with indistinct cusps, and finely wrinkled, deeply basined trigon are features in common, suggesting that the two taxa may be congeneric. That they are distinct at species level is indicated by the absence of a hypocone on the Avenay upper preultimate molar.

Michaux (1968) did not place his 'genre indéterminé B' in any paramyid subfamily. The suggestion that the present form might be a manitshine is based on its vague similarity to *Plesiarctomys*.

A rodent lower right incisor from Creechbarrow (M37190) (Text-fig. 30F–I) fits none of the other taxa described here, unless it is a juvenile *Ailuravus*. It is the correct size for the present form, and has some unusual features. It is an almost symmetrically compressed D-shape in cross section and has a buccolingually elongated pulp cavity, not triangular or dagger-shaped as in *Plesiarctomys*. There is a single distobuccal carina. The enamel is as thin as in the incisors of *Ailuravus*. The mesial enamel band extends one fifth of the width (buccolingual) of the tooth. Distally the enamel extends more than half way round the tooth. From figures in Wood (1962) this degree of enamel extension occurs in *Ischyrotomus compressidens* (Peterson 1919), *Reithroparamys debequensis* Wood 1962, *Leptotomus sciuroides* (Scott & Osborn 1890), *L. mytonensis* Wood 1962, *L. bridgerensis* Wood 1962, *L. parvus* Wood 1959, *L. huerfanensis* Wood 1962, *L. costilloi* Wood 1962, *L. grandis* Wood 1962, *L. leptodus* (Cope 1883), *Paramys delicatior* Leidy 1873 and *P. delicatus* Leidy 1873 amongst the North American paramyids and *Ailuravus* spp. amongst the European ones. It does not occur, however, in *Paramys francesi*, the species that Michaux (1968: 175) considered closest to his 'genre indéterminé B'. This could be a primitive character of no importance in isolation, or M37190 may not belong to the same species as the other teeth assigned to the present form.

Subfamily **AILURAVINAE** Michaux 1968

Diagnosis. See Wood, 1976*a*: 122.

Genus ***AILURAVUS*** Rütimeyer 1891

[incl. *Palaeomarmota* Haupt 1921, *Megachiromyoides* Weigelt 1933, *Aeluravus* and *Maurimontia* Stehlin & Schaub 1951]

Type species. *Ailuravus picteti* Rütimeyer 1891. Late Lutetian fissure fillings, Egerkingen, Canton Solothurn, Switzerland.

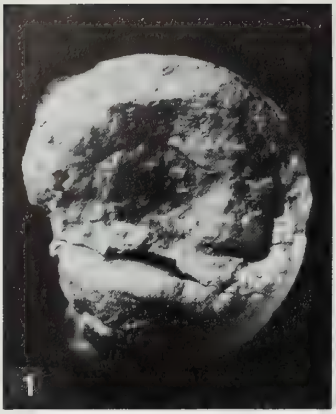
Included species. *A. michauxi* Hartenberger 1975, *A. macrurus* Weitzel 1949, *A. stehlinschaubi* Wood 1976*a*.

Range. Late Ypresian to Bartonian; Britain, France, East and West Germany and Switzerland.

Emended diagnosis. See Wood, 1976*a*: 123–124.

Remarks. Following Wood (1976*a*: 145) it is considered that the two species described but not named by Michaux (1968: 159–161) fall within the variation of a single species. They were later named by Hartenberger (1975: 780–781) but his diagnoses do not allow them to be distinguished and no measurements were given. Therefore, *A. remensis* Hartenberger 1975 (p. 781) is herein synonymized with *A. michauxi* Hartenberger 1975 (p. 780) on page priority.

The four species listed above are not easy to distinguish because of the small number of specimens of each species and the large amount of individual variation. Even though *A. macrurus* is known from complete skeletons with fur preserved, the teeth are usually in occlusion and cannot easily be seen. Creechbarrow is only the second known locality for *A. stehlinschaubi* and considerably increases the number of teeth known. DP^3, P^3, DP_4, I^1 and I_1 were previously unknown.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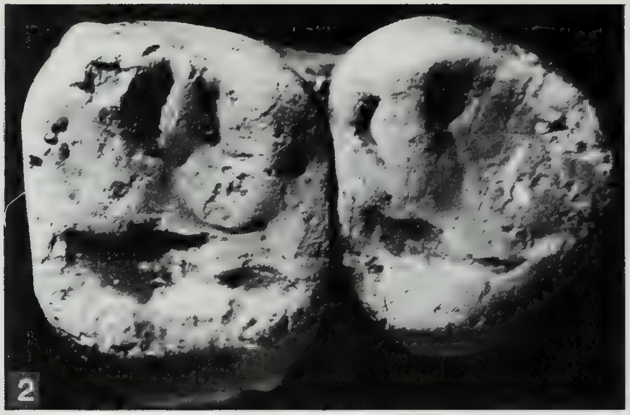
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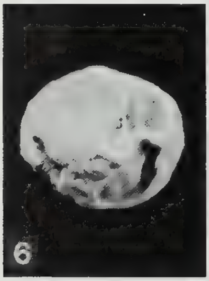
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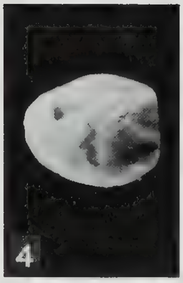
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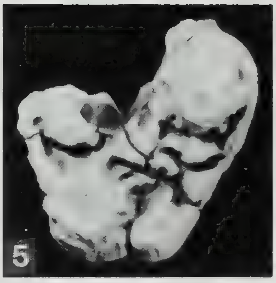
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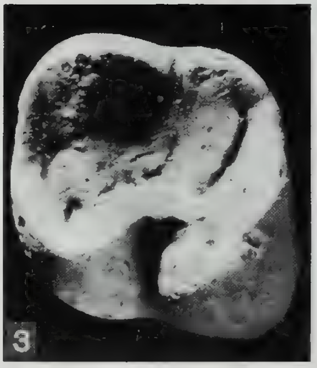
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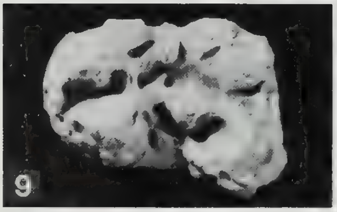
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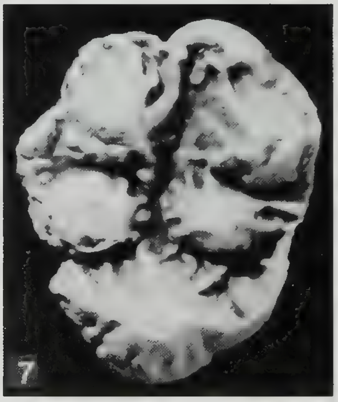
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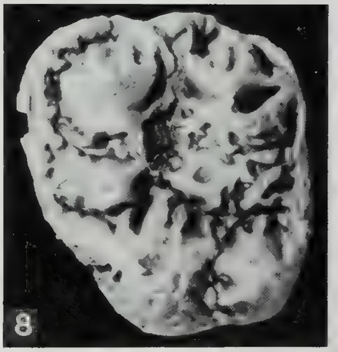
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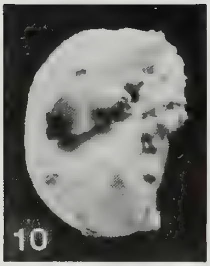
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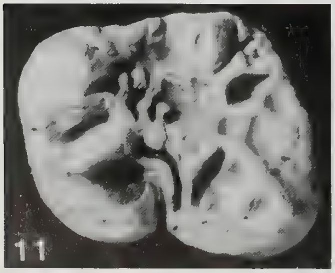
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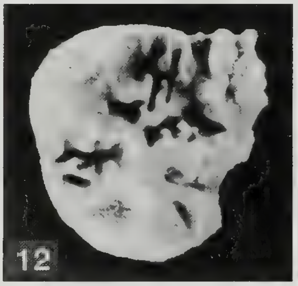
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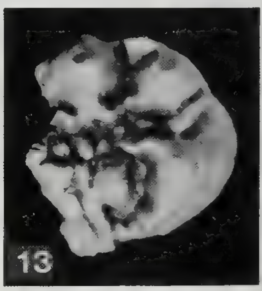
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Ailuravus stehlinschaubi Wood 1976*a*
(Pl. 14, figs 4–13; Text-fig. 30J–K; Table 12)

v. 1869 *Hyracotherium* Owen?; ?Pictet & Humbert: pl. 25, fig. 5.
v. 1951 *Maurimontia picteti* Stehlin & Schaub: 20, fig. 18; 206, fig. 310.
v. 1962 *Maurimontia picteti* Stehlin & Schaub; Wood: 239, fig. 88G–H.
v* 1976*a* *Ailuravus stehlinschaubi* Wood: 141–145, fig. 6.
v. *1977b* *Ailuravus stehlinschaubi* Wood; Hooker: 141–142.
v. *1980* *Ailuravus stehlinschaubi* Wood; Hooker & Insole: 39.

HOLOTYPE. Right maxilla with DP^4, P^4–M^3 (LGM 39559: LM 2906). Bartonian fissure filling, Eclépens-Gare, Canton Vaud, Switzerland.

PARATYPES. Right mandibular ramus with chipped P_4–M_3 (LGM 39561: LM 2910), and left M^1 (NMB Mt1767). Occurrence as holotype.

MATERIAL. DP^3 (M35453); P^3 (M35769); DP^4 (M35771); 3 P^4s (M35770, M37191–2); 6 $M^{1/2}$s (M35454–6, M35772, M37193, M37697); 2 DP_4s (M35774–5); $M_{1/2}$ (M35457); 8 trigonid and talonid fragments of $P_4/M_{1/2}$ (M35458–9, M35776–8, M35780, M37194, M37698); M_3 trigonid (M35779) and talonid (M35773) fragments; 12 undetermined fragments of cheek teeth (M35460–3, M35784, M37195); I^1 (M35698); and 6 I_1s (M35781–3, M37196–8).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

RANGE. Recorded only from the Bartonian of Eclépens-Gare, Switzerland; and Creechbarrow, England.

EMENDED DIAGNOSIS. (Slightly modified from Wood, 1976*a*: 142). Large species of *Ailuravus*, length of M^1 = 4·50–5·14 mm (see also measurements in Table 12 and Wood, 1976*a*: 127); cusps (especially conules) of upper cheek teeth tend to be elongate mesiodistally; valleys between cusps deep; enamel wrinkling moderate to dense; single paraconule; metaconule developing a mesio-distal elongation or doubling; protostyle weak to missing; mesostyle very prominent and buccally extended, especially on P^4; M^{1-2} with hypocone consistently only slightly smaller than protocone; M^3 without hypocone; mesoconid of lower teeth very large, triangular, and cut off from buccal margin of tooth; posterolophid of molars almost non-existent except for the hypertrophied hypoconulid; incisors almost circular in cross section and small (I_1 mesiodistal dimension 40–52% of $M^{1/2}$ length); mental foramen more than the length of P_4 in front of P_4.

DIFFERENTIAL DIAGNOSIS. *A. michauxi* is smaller with cone-shaped intermediate conules on upper cheek teeth; valleys shallow with much less enamel wrinkling; paraconule may be double; protostyle prominent; mesostyle and hypocone smaller; molar posterolophid more continuous; [incisors and jaw unknown].

A. macrurus has cone-shaped intermediate conules; valleys shallow with much less enamel wrinkling; paraconule double; protostyle prominent; mesostyle smaller; hypocone may be smaller; molar posterolophid more continuous; incisors more buccally tapered and slightly larger; mental foramen more posterior.

A. picteti has less elongate intermediate conules; valleys may be shallower and may have less enamel wrinkling; paraconule double; protostyle may be prominent; mesostyle smaller; hypo-

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Plate 14 Light macrographs of occlusal views of cheek teeth of paramyids from Creechbarrow, × 8.

Figs 1–3 *Plesiarctomys hurzeleri* Wood. Fig. 1, left P^4 (M35761). Fig. 2, right M^{2-3} (reversed) (M37185). Fig. 3, left M_1 (M37187). See p. 288.

Figs 4–13 *Ailuravus stehlinschaubi* Wood. Fig. 4, right DP^3 (reversed) (M35453). Fig. 5, left DP^4 (M35771). Fig. 6, left P^3 (M35769). Fig. 7, left P^4 (M37191). Fig. 8, right $M^{1/2}$ (reversed) (M37193). Fig. 9, left DP_4 (M35775). Fig. 10, left P_4? trigonid fragment (M35778). Fig. 11, right $M_{1/2}$ (reversed) (M35457). Fig. 12, left M_3 trigonid fragment (M35779). Fig. 13, left M_3 talonid fragment (M35773). See above.

Table 12 Length (l) and mesial (w_1) and distal (w_2) width measurements of *Ailuravus stehlinschaubi* from Creechbarrow. Only one width measurement is given for incisors and upper cheek teeth. Measurements in millimetres.

No.	Tooth	l	w_1		w_2
M35453	DP^3	2·30		1·85	
M35769	P^3	2·70		2·35	
M35770	P^4	(5·20)		–	
M37191	P^4	(5·70)		6·30	
M37192	P^4	5·35		–	
M35454	M^1?	4·50		–	
M35772	M^1?	4·75		5·55	
M37193	M^1?	4·95		5·60	
M37697	M^2?	4·75		5·25	
M35774	DP_4	(4·50)	3·10		(3·60)
M35775	DP_4	4·20	(2·60)		(3·25)
M35778	P_4?	–	3·45		–
M35780	P_4?	–	3·45		–
M37698	P_4?	–	–		3·75
M35457	$M_{1/2}$	4·90	3·80		4·35
M35458	$M_{1/2}$	–	3·45		–
M37194	$M_{1/2}$	–	3·65		–
M35459	$M_{1/2}$	–	–		4·30
M35776	$M_{1/2}$	–	–		4·15
M35779	M_3	–	4·00		–
M35773	M_3	–	–		3·55
M35698	I^1	2·60		2·40	
M35781	I_1	2·05		2·60	
M35782	I_1	2·15		(2·90)	
M35783	I_1	2·05		(2·90)	
M37196	I_1	2·00		2·35	
M37197	I_1	2·30		2·85	
M37198	I_1	2·35		2·95	

cone may be smaller; mesoconid usually joined to hypoconid by buccal spur as well as by ectolophid; incisors slightly larger (inferred from alveoli); mental foramen more posterior.

DESCRIPTION. Wood (1976*a*) has described this species in detail, so only new features or variations will be dealt with here. Most of the tooth measurements of the Creechbarrow material are slightly less than their counterparts in the type series (see Table 12 and Wood, 1976*a*: 126–127, tabs 1–2).

Wrinkling of the enamel is very variable in extent and detail. It may be relatively weak (Pl. 14, fig. 7) or very strong (Pl. 14, fig. 8). It usually has a narrow core of dentine. Because of the variation, there is overlap with *A. picteti*, but here the degree of wrinkling is usually less.

DP^3 and P^3 (Pl. 14, figs 4, 6): Wood (1976*a*: 143–144) suggested that these teeth were probably absent in the holotype, referring to the absence of alveoli in Stehlin & Schaub's (1951) fig. 18, drawn before jaw breakage caused by DP^4 removal. However, Pictet & Humbert's (1869: pl. 25, fig. 5b) buccal view shows the maxilla to have been truncated immediately anterior to DP^4. The question can never be settled for the holotype, but M35453 and M35769 show the morphologies of DP^3 and P^3 respectively and indicate that both these teeth could occur in *A. stehlinschaubi*. M35453 is the smaller and has much thinner enamel than M35769 or any of the P^4s or molars, which is typical for a milk tooth. It has a prominent parastyle, distally placed ?paracone with two distal crests, a minute ?protocone at the distolingual corner and a ?preparacrista with a small cuspule at about its midpoint. M35769 is narrower distally, has a central paracone with a buccally flexed postparacrista which joins a distal cingulum bearing a small lingual cuspule; a curved crest runs down the lingual side of the paracone; there is neither parastyle nor protocone.

DP^4 (Pl. 14, fig. 5): This tooth is broken mesiobuccally but is essentially similar to that of the holotype DP^4.

P^4: M37191 is lacking most of the parastyle but from the spacing of its main cusps seems to be relatively broader than the holotype P^4, has slightly more wrinkled enamel and a small hypocone (Pl. 14, fig. 7). M35770 has the protocone broken away and is much more densely wrinkled than either M37191 or the holotype. M37192 is heavily, naturally worn and shows a similar degree of wrinkling to M37191.

$M^{1/2}$: M^1 and M^2 of the holotype can be distinguished on length/width ratio. Among the isolated Creechbarrow upper preultimate molars, the shorter broader ones are tentatively identified as M^1 and the single relatively longer one as M^2. There is high variation in enamel wrinkling, buccal cingulum strength and mesostyle size. There are also differences in the distal elongation or doubling of the metaconule: in M35772 and M37697 there is a second metaconule developed distal to the first; in M35454 and M35455, the first metaconule has a strong distal crest extending to the distal cingulum; and in M37193, the whole area distal to the first metaconule is covered with dense enamel wrinkling (Pl. 14, fig. 8).

DP_4 (Pl. 14, fig. 9): Two submolariform teeth (M35774 and M35775) have thinner enamel than any of the molars and so are identified as DP_4, a tooth not previously recorded for the genus *Ailuravus*. They show variation in degree of enamel wrinkling, as do the molars. The principal differences from the holotype P_4 are presence of a smaller, rounder, less triangular mesoconid, large isolated lingually situated hypoconulid, an extensive cingulum-bordered sinusid and lower crown height.

Lower Permanent Cheek Teeth: Only the $M_{1/2}$, M35475, is complete (Pl. 14, fig. 11). All the others are either trigonid or talonid fragments. The M_3 talonid (M35773) shows, better than the poorly preserved paratype, the crescentically crested hypoconid and the almost total isolation of this cusp, the hypoconulid, entoconid and mesoconid (Pl. 14, fig. 13). The trigonid (M35779) is identified as M_3 because of the distal position of the protoconid relative to the metaconid and the apparent depth of the ectoflexid (Pl. 14, fig. 12). The remaining talonid fragments add little to our existing knowledge of the species. Of the trigonids, those with the more convergent cusps are tentatively identified as P_4 (e.g. Pl. 14, fig. 10) from comparison with the admittedly imperfect paratype premolar and molars.

Incisors: The finding of seven *Ailuravus* incisors at Creechbarrow is in marked contrast to the normal rarity of these teeth (see Wood, 1976*a*: 125). The cross-sectional shape of the lowers is similar to that of *A. macrurus* figured by Wood (1976*a*: fig. 5G), but rounder (Text-fig. 30K). The single upper is also much rounder than Wood's (1976*a*: fig. 5D) figured I^1 of *A. macrurus* (see Text-fig. 30J).

Discussion. Although not recorded from other localities, it is possible that the record of Ailuravinae gen. indet., which is an incisor (J.-L. Hartenberger, personal communication 1978), from Robiac (Sudre 1969*a*: tab. opposite p. 142) might be shown to belong to this species if cheek teeth can be found.

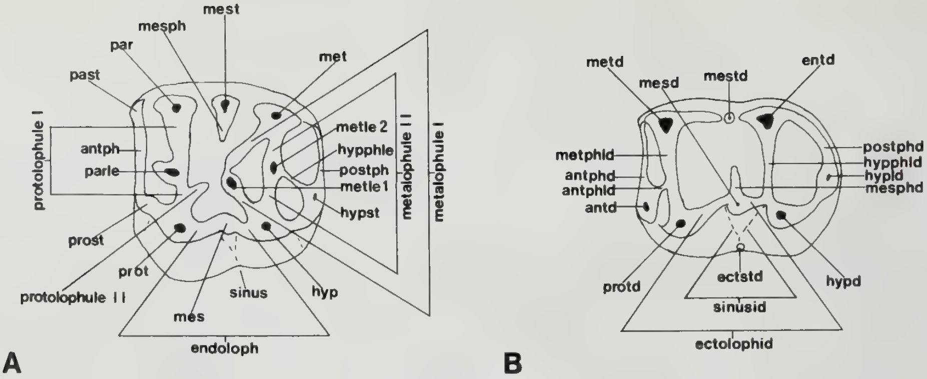
Wood (1976*a*: 145) considered *A. stehlinschaubi* to have descended from Lutetian *A. picteti*. The *Ailuravus* sp. indet. from the Auversian Sables à *Batillaria bouei* (Sables d'Auvers) of Arcis-le-Ponsart, Marne, France, may provide an intermediate between the two (Louis 1976: 49).

Thus *A. stehlinschaubi* is a good age marker for the European Bartonian, if not more strictly the Marinesian. The genus appears to have become extinct at the end of the Bartonian.

Infraorder uncertain

Superfamily **THERIDOMYOIDEA** Alston 1876

This superfamily has been classifed in various ways infraordinally in the Rodentia (e.g. Schaub 1958, Romer 1966, Simpson 1945), but it is probably derived from subfamily Paramyinae of the



Text-figure 31 Dental nomenclature of pseudosciurid cheek teeth. A, left upper molar. Buccal edge towards top of page, lingual towards bottom. B, left lower molar. Buccal edge towards bottom of page, lingual towards top.

Abbreviations:

A. antph—anteroloph
hyp—hypocone
hypphle—hypolophule
hypst—hypostyle
mes—mesocone
mesph—mesoloph (partial)
mest—mesostyle
met—metacone
metle 1—metaconule 1
metle 2—metaconule 2
par—paracone
parle—paraconule
past—parastyle
postph—posteroloph
prost—protostyle (= anterocone)
prot—protocone

B. antd—anteroconid
antphd—anterolophid
antphld—anterolophulid
ectstd—ectostylid
entd—entoconid
hypd—hypoconid
hypld—hypoconulid
hypphld—hypolophulid
mesd—mesoconid
mesphd—mesolophid (partial)
mestd—mesostylid
metd—metaconid
metphld—metalophulid
postphd—posterolophid
protd—protoconid

Paramyidae (see Hartenberger 1969: 56). No evidence is forthcoming on these questions from the English Bartonian material. Suffice to say that theridomyoids are hystricomorphous and sciurognathous and have cheek teeth which range from low-crowned to moderately high-crowned but always retain the roots. The complexities of convergence in hystricomorphy are discussed by Wood & Patterson (1970). Their dental formula is $\frac{1\ 0\ 1\ 3}{1\ 0\ 1\ 3}$ but sometimes DP$\frac{4}{4}$ is retained and not replaced by P$\frac{4}{4}$.

They have usually been divided into two families: the Pseudosciuridae Zittel 1893 for the lower-crowned and Theridomyidae Alston 1876 for the higher-crowned types. However, Hartenberger (1971) produced a model of parallel evolution of higher-crowned forms (which would have been classified as theridomyids) from new (*Estellomys*) and hypothetical lower-crowned forms (which would have been classified as pseudosciurids or as transitions between the two families). He assimilated the two families under the name Theridomyidae which he divided into six subfamilies, all considered to be monophyletic. These were later increased to seven (Hartenberger 1973) and comprised: Pseudosciurinae Zittel 1893, Oltinomyinae Hartenberger 1971, Sciuroidinae Hartenberger 1971, Columbomyinae Thaler 1966, Theridomyinae Alston 1876, Issiodoromyinae Lavocat 1951 and Remyinae Hartenberger 1973, with the genus *Quercimys* Thaler 1966 of uncertain family status. *Tarnomys* was described later (Hartenberger & Schmidt-Kittler 1976), but although considered related to *Pseudosciurus*, it was classified at no lower level than superfamily Theridomyoidea. The Pseudosciurinae and Sciuroidinae contained all the genera which had been included in the Pseudosciuridae before 1973. Bosma (1974) accepted the traditional separation of the Pseudosciuridae and Theridomyidae and considered that Hartenberger's transition forms should be placed arbitrarily in one or the other family. She did not recognize the subfamily division of the Pseudosciuridae (presumably meaning the Pseudosciurinae and Sciuroidinae) but gave no further explanation.

This division into two subfamilies is untenable for the following reasons. Hartenberger (1973) described a new species of *Suevosciurus* (*S. romani*) in the Pseudosciurinae which in fact is identical with *Sciuroides siderolithicus*, type species of the type genus of the Sciuroidinae. Therefore the type species of *Sciuroides* was included in both the Pseudosciurinae and Sciuroidinae. Apart from *S. siderolithicus*, which was not treated systematically, all the other *Sciuroides* species which he put in the Sciuroidinae are, according to Bosma (1974), referrable to *Paradelomys*; see details below. Only one of Hartenberger's diagnostic features for the two subfamilies allows comparison: the size of the anterior palatal foramina, and here there is much overlap.

From Hartenberger's (1973) text-fig. 2, only one lineage in his Theridomyidae is shown to have evolved from truly brachyodont to hypsodont and thus bridged his 'Pseudosciuridae'/'Theridomyidae' grade boundary. This is the *Estellomys–Oltinomys* lineage.

The principle of evolution of high-crowned from low-crowned forms is not in doubt here. It is a common and well documented trend among fossil mammals. Even if this happened in parallel, however, no forms originally placed in the Pseudosciuridae have necessarily given rise to any originally placed in the Theridomyidae. Problems in classification always occur when the stem of two suprageneric groups such as these is approached. It is not necessarily solved, however, by lumping the two groups. In post-Bartonian time there are two well-defined groups which differ considerably in crown height and must have occupied very different ecological niches. It seems desirable to recognize these as different families and seek more reliable characters to define each. Three combined features which characterize all the higher-crowned forms plus *Estellomys* are: 1, a mesoloph which tends to join the hypocone; 2, absence of a metalophule I; and 3, an oblique ectolophid without mesoconid. Conversely the Pseudosciuridae have lesser or greater tendencies towards: 1, mesoloph not joined to hypocone; 2, presence of metalophule I independent of the mesoloph; and 3, presence of mesoconid.

The characters outlined above support the retention of these two families, but pose problems for *Paradelomys* and *Tarnomys* which are somewhat intermediate. All the species except typical *P. crusafonti* have a metalophule I, although in the late forms (*P. spelaeus* and *T. quercinus*) it sometimes partially fuses with the mesoloph (see Schmidt-Kittler 1971*a*: fig. 27). However, the earliest assemblage known of *P. crusafonti* (that of Grisolles) has a metalophule I and a short mesoloph. It is evident that the long, but weak, mesoloph which joins the hypocone in assemblages from Robiac times onward is formed by fusion of the short buccal mesoloph to the lingual half of metalophule I, with abortion of the distobuccal half of metalophule I. All the theridomyids may also have undergone a similar modification and the genera here attributed to the Pseudosciuridae may be only those that retained it as a primitive feature. Nevertheless, unlike *P. crusafonti*, typical theridomyids all show a strong hypocone-joining mesoloph. This is more likely to have been derived from a morphology like that occurring in Lutetian *Protadelomys alsaticus* Hartenberger 1969. Some individuals of this species (Hartenberger 1969: pl. 2, figs 4, 7) have a long, strong mesoloph joining the metaconule, which suggests a trend towards the Theridomyidae as construed here.

Paradelomys as defined by its type species alone, *P. crusafonti*, had developed its deep sinus by at least the Bartonian, but still had an oblique ectolophid and no anterolophulid or mesoconid. Three other species that have been referred to *Paradelomys* (*P. depereti*, *P. quercyi* and *P. spelaeus*) have a metalophule I, non-oblique ectolophid, weak mesoconid, antesinusid and anterolophulid. They might usefully be placed in a new genus.

None of the brachyodont theridomyoids that developed metalophule I are known to have given rise to hypsodont taxa, but all that instead developed a strong mesoloph–hypocone link did give rise to hypsodont taxa. This tends to justify the retention of both families as probably monophyletic natural adaptive groups. If it should be found, however, that the characters used to differentiate them were independently evolved, then a modifed system of Hartenberger's subfamilies might prove to be a suitable solution, or different characters again might be used to differentiate the two families.

Family **PSEUDOSCIURIDAE** Zittel 1893

TYPE GENUS. *Pseudosciurus* Hensel 1856.

INCLUDED GENERA. *Protadelomys* Hartenberger 1968, *Sciuroides* Major 1873, *Treposciurus* Schmidt-Kittler 1970, *Suevosciurus* Dehm 1937, *Paradelomys* Thaler 1966 and *Tarnomys* Hartenberger & Schmidt-Kittler 1976.

RANGE. Lutetian to Stampian; England, Belgium, France, Spain, Switzerland and West Germany.

EMENDED DIAGNOSIS. Cheek teeth brachyodont; uppers with metalophule I and/or with rugose to reticulate enamel and only short mesoloph; lowers with mesoconid and/or with bent ectolophid.

TAXONOMIC TREATMENT. Pseudosciurids are represented at Creechbarrow by single species of *Sciuroides*, *Treposciurus* and *Suevosciurus*. They are abundant as individuals and the *Suevosciurus* comprises more than 20% of the total mammal fauna. Because of the varied generic and specific combinations which have been proposed within this family, the maximum number of available characters has been used in a stratigraphical context to minimize the confusing effects of evolutionary reversals and parallelisms. Often these characters are not present in all individuals, infraspecific variation being high. Their percentage occurrences are tabulated in order, to avoid as much as possible use of imprecise words like 'usually' and 'most', which however still need to be used in the generic diagnoses. Equally important as a taxonomic method in the face of such large morphological variation is the estimation of coefficients of size variation. In any one assemblage low coefficients of variation for tooth size give confident species limits (see Gingerich 1974).

DENTAL NOMENCLATURE (Text-fig. 31). Bosma (1974: 16–17) stated that she was following Wood & Wilson (1936) for her nomenclature of the dental pattern. She did not in fact closely follow these authors, possibly because their terminology was designed for only cricetid, heteromyid and sciuravid, not theridomyoid, teeth. Moreover, in Bosma's (1974) text-fig. 2, of a labelled pseudosciurid right upper molar, some of the cusp names have been transposed as if the tooth were a left. These errors are repeated in Bosma & Insole (1976: 2, text-fig. 1). Hartenberger (1973: 6) stated that he was directly following Wood & Wilson (1936) and Schaub (1958) (the latter presumably only for the higher crowned types), but his system differs somewhat from that of Bosma and more closely resembles that of Wood & Wilson for a cricetid type of tooth. I essentially follow Wood & Wilson's and Hartenberger's schemes with the following exceptions:

1, I use paraconule instead of protoconule to maintain uniformity of nomenclature for all mammals with this cusp. The choice is because the paraconule has the same spatial relationship to the paracone, not to the protocone, as the metaconule has to the metacone. 2, I tentatively recognize a mesocone. 3, Bosma (1974) named the loph joining the metacone to the hypocone the metaloph, and the intermediate conule on it the metaconule. The more mesial parallel loph she called metalophule I, from Wood & Wilson (1936). Hartenberger used Wood & Wilson's term metalophule II for Bosma's metaloph but retaining her meaning of metaconule. In post-Lutetian pseudosciurids, there are often two distal lophules on upper molariform teeth, which can be homologized or at least compared for identity of position with metalophules I and II of the cricetid type (Wood & Wilson 1936: 389, fig. 1). Both or either may bear or be reduced to a conule. Of these only the more distal one has been named – the metaconule. In Lutetian pseudosciurids and the presumed ancestral paramyids with tribosphenic teeth, there is a single cusp occasionally on a single crest between metacone and protocone. It can easily be homologized with the metaconule. Individual variation in this region in species of *Protadelomys* as illustrated by Hartenberger (1969) shows incipient development of two lophules and two conules, all derived from or developed around the original metaconule. Therefore metaconule 1 herein is the previously unnamed cusp on or replacing metalophule I, whilst metaconule 2 is the metaconule of Bosma and Hartenberger. 4, I tentatively recognize a hypostyle as the swelling on the posteroloph. 5, the enamel bridge which sometimes links metalophule II to the posteroloph I name the hypolophule. 6, The crest, which sometimes trends distobuccally from the protocone, I consider can be referred to an incipient protolophule II. 7, I recognize the anterolophulid as used by Mein & Freudenthal (1971: 3) for cricetid teeth.

DEVELOPMENT OF METALOPHULE I. There is variation in the position of the lingual attachment of metalophule I in pseudosciurids. The condition in upper first and second molars is as follows. In *Sciuroides* it ranges between the lingual half of metalophule II and half way between the middle of the endoloph and the hypocone. In *Treposciurus*, it ranges between the middle of the endoloph and half way between this point and the hypocone. In *Suevosciurus* (vestigially), *Tarnomys* and *Paradelomys* it is predominantly close to or immediately distal to the middle of the endoloph. In DP^4, the lingual attachment in all these genera has the same range as in the M^{1-2} of *Sciuroides*. *Pseudosciurus* has no metalophule I. Late members of the respective genera tend to have a lingual attachment intermediate between the hypocone and the middle of the endoloph, whereas in early members it is at opposite extremes away from this position. Thus there appears to be a time-linked trend towards the intermediate position as the 'optimum'; and a slightly different mode of origin of an otherwise homologous structure.

It appears therefore that, in $M^{1\ 2}$ of *Sciuroides* and in DP^4 of all the genera, the metaloph begins to split from the buccal end. It is not until the split has progressed right to the endoloph that the 'optimal' position is reached. Some support for this hypothesis is provided by *Protadelomys lugdunensis* Hartenberger 1969, from the Auversian of Lissieu and shown by Hartenberger (1969) to be closely related to *Sciuroides* (under the name of *Suevosciurus*). *P. lugdunensis* has an undivided metaconule but two crests link it to the metacone and only one to the hypocone (Hartenberger 1969: pl. 4, figs 2–3).

Metalophule I in $M^{1\ 2}$ of the other genera appears to have developed as a crest along the line of the postprotocrista, as the metaconule split in response to the expansion of the distolingual portion of the tooth. That this may have developed fairly rapidly from a morphology closely resembling that of *Protadelomys cartieri* from the late Lutetian of Egerkingen γ (see Hartenberger 1969: pl. 1, fig. 1) is suggested by an unusual individual within the morphologically very variable assemblage of *Treposciurus helveticus preecei* from Creechbarrow. This $M^{1/2}$ (Pl. 18, fig. 8) has no metalophules but a single massive metaconule in a position which would be intersected by a straight line drawn between the protocone and metacone. It is thus slightly more mesial than the metaconule in *P. lugdunensis*. Other variants show different grades of development of the metalophules, mainly I, which nearly always either joins, or is very close to, the middle of the endoloph, where a mesocone is often present.

Thus the most primitive genus in the Pseudosciuridae (*Protadelomys*) lacks metalophule I and could be regarded as providing potential ancestors for both theridomyoid families. As discussed above, important characters are shared between *P. alsaticus* and typical Theridomyidae and between *P. lugdunensis* and typical Pseudosciuridae. More specimens from Lutetian–Auversian sites may eventually result in the splitting up of the genus *Protadelomys*, but it is here provisionally retained undivided within the Pseudosciuridae.

NOTE ON ENAMEL WRINKLING. A character of frequent occurrence in the Pseudosciuridae is wrinkling of the enamel. Even at their strongest the wrinkles are not dentine-cored and have often been removed by natural tooth wear. Their pattern may vary, from isolated granules, to a series of ridges, to reticulation. They have been mapped in detail for *Pseudosciurus* by Schmidt-Kittler (1971*a*). The wrinkling may be coarse to fine, low or high, extensive or restricted to only some areas of the tooth. Complicated as they may seem these various features are directly related to the intensity of the wrinkling. Slight wrinkling (grade 1 of the character analysis tables 14–15, 17–18, 20–21) produces low, isolated granules; more intense wrinkling (grade 2) produces a system of ridges; and the maximum observable intensity (grade 3) produces a high reticulate pattern which fills the tooth valleys, leaving deep circular cavities between. Fineness and coarseness vary independently of these grades and together with wear make objective comparisons difficult, but they are nevertheless attempted for the three pseudosciurids from Creechbarrow and their relatives.

IDENTIFICATION OF ISOLATED PREULTIMATE MOLARS. Isolated first and second molars are difficult to distinguish from one another, but those uppers with near square outline are regarded as M^1 and those with distally tapering outline as M^2; mesially tapering lowers are identified as M_1 and those which are rectangular as M_2. These identifications are only tentative and are attempted for the purposes of the percentage character analysis tables only, where expression of characters in each tooth morphology is important. In the tables and graphs of length and width measurements they are not separated, but nevertheless still produce sufficiently low coefficients of variation.

Genus ***SCIUROIDES*** Major 1873

TYPE SPECIES. *Sciurus siderolithicus* Pictet & Humbert 1869. Marinesian fissure filling, Eclépens-Gare, Canton Vaud, Switzerland.

INCLUDED SPECIES. *S. russelli* (Hartenberger & Louis 1976), *S. ehrensteinensis* Schmidt-Kittler 1971*a* and *S. rissonei* sp. nov.

RANGE. Marinesian; England, France, Switzerland. Ludian; England, Switzerland and ?France.

EMENDED DIAGNOSIS. Upper cheek teeth with: high endoloph; strong, dentine-cored, complete to incomplete metalophule I; strong paraconule; presence of a metaconule 2; DP^4 with straight mesiolingual margin and unicuspid parastyle. Lower cheek teeth with: high, complete, straight oblique to bent ectolophid joining hypolophulid separately from hypoconid; weak mesoconid. Lower molars with: small to large, often median anteroconid on M_{1-2}; anterolophulid usually present; anterolophid weak; metalophulid low and incomplete. DP_4 with: crown height lower than that of molars; metalophulid absent. M_3 hypolophulid high and complete. Anterior palatine foramina project just posterior to maxillary–premaxillary suture (known only for *S. siderolithicus*).

PREVIOUS DIAGNOSES. Major (1873) gave no formal diagnosis and Schlosser (1884: 76–77) was the first to give an adequate description. Major's concept of the genus included species now included in other pseudosciurid genera (see Dehm 1937; Schmidt-Kittler 1971*a*). Schmidt-Kittler (1971*a*: 29) gave a brief history of treatment of the genus and a comprehensive diagnosis.

Hartenberger (1973: 21) did not discuss Schmidt-Kittler's diagnosis or concept of *Sciuroides*, but gave his own short diagnosis: 'Crête longitudinale joignant protoconide et hypoconide assez développée. Présence presque constante aux molaires supérieures d'un metalophule I'. Thus his own new species, *Suevosciurus* (*Treposciurus*) *romani*, fits this diagnosis and is in fact inseparable from the type species of *Sciuroides*. Hartenberger included in *Sciuroides* (apart from the type species) '*S.*' *quercyi*, '*S. intermedius*' and '*S.*' *ruetimeyeri*. He incorporated *Sciuroides* and *Paradelomys* into his subfamily Sciuroidinae. One of his characters of this subfamily was medium to large anterior palatine foramina. '*S.*' *quercyi* and '*S. intermedius*' (= '*Paradelomys*' *depereti*, see Bosma 1974: 54) fit the medium category; those of '*S.*' *ruetimeyeri* are unknown; and those of the type species of *Sciuroides* are short and thus prevent its inclusion in the type subfamily.

In contrast, Schmidt-Kittler's (1971*a*) concept of *Sciuroides* produces no anomalies and *Suevosciurus russelli* Hartenberger & Louis 1976 can readily be accommodated in it. Slight emendations and additions are made above and involve the following points. 1. Schmidt-Kittler (1971*a*: 29 and table 4) distinguished *Sciuroides* from the other pseudosciurid genera by the absence of enamel wrinkling. This was based on the few available specimens of *S. siderolithicus* and the unique $M^{1/2}$ of *S. ehrensteinensis*. Bosma (1974: 32–33) described further material of the latter from the Headon Beds of the Isle of Wight and noted that the enamel was slightly rugose. In some individuals of all four species there may be minor unnamed crests branching from the major lophs as well as numerous irregularities of the enamel but they tend to be coarser than those which occur in *Treposciurus* or *Suevosciurus*. Enamel wrinkling is thus not of generic significance. 2, The weakness of the anterolophid and metalophulid is an important character not previously mentioned.

EXCLUDED SPECIES. 1. *Adelomys* (*Sciuroides*) *fontensis* Thaler 1966, from the early Ludian of Fons 1. Schmidt-Kittler (1971*a*: 35) thought it was probably synonymous with *S. siderolithicus*. Hartenberger (1973: 29) doubted that it was even a pseudosciurid. It has the interrupted metalophulid of *Sciuroides* and is about the size of *S.* aff. *siderolithicus* from Weidenstetten. Without more material its status is problematical.

2. *Suevosciurus* (*Treposciurus*) *romani* Hartenberger 1973, from the late Bartonian of Robiac. Bosma (1974: 33) put it in *Sciuroides*. Comparison of casts of Hartenberger's figured specimens with the type series of *S. siderolithicus* and referred material from the Quercy Phosphorites in the BM(NH) has shown no tangible differences. UM RBN900 (P^4–M^1 according to Hartenberger 1973: pl. 2, fig. 1) is reidentified as DP^4–M^1 because of the large parastyle and distinct paraconule of the DP^4. The species is here synonymized with *S. siderolithicus* and the Robiac specimens are considered good confirmatory evidence of the Bartonian age of Eclépens-Gare.

3. *Sciuroides intermedius* Schlosser 1884. Schmidt-Kittler (1971*a*) placed this species in his genus *Treposciurus*. The material which Hartenberger (1973: 22) referred to *S. intermedius* is *Adelomys depereti* Stehlin & Schaub 1951 (see Bosma 1974: 54).

4. and 5. *Adelomys depereti* Stehlin & Schaub 1951 and *Sciuroides quercyi* Schlosser 1884. Bosma (1974: 55) placed both in *Paradelomys*. They cannot be *Sciuroides* because they have a deep mesially-directed sinus and its closure buccally (when present) can be shown to be composed of the lingual end of metalophule I fused with incipient protolophule II. This closure is thus not homologous with the strong shallowly-indented endoloph of *Sciuroides*.

6. *Sciurus ruetimeyeri* Pictet & Humbert 1869. This species was referred by Hartenberger (1973: 21) to *Sciuroides*. Schmidt-Kittler (1971*a*: 72–73) thought it should go in a genus of its own while retaining it as '*Sciuroides*' *rütimeyeri* (sic). As interpreted by the better preserved of the two figured syntypes (Pictet & Humbert 1869: pl. 14, fig. 7) (LGM 40464: LM 2930), it is a species of *Paradelomys* very similar to and possibly conspecific with *P. crusafonti*. The upper molar from Eclépens B identified by Schmidt-Kittler (1971*a*: text-fig. 28) as '*Sciuroides*' *rütimeyeri* fits better with *Paradelomys depereti*.

Sciuroides rissonei sp. nov.

(Pl. 15; Text-figs 32–33; Tables 13–15)

v. 1977*b* *Sciuroides* cf. *russelli* (Hartenberger & Louis); Hooker: 141.
v. 1980 *Sciuroides* aff. *russelli* (Hartenberger & Louis); Hooker & Insole: 39.

NAME. After Mr A. Rissoné for help with field work.

HOLOTYPE. Right $M_{1/2}$ (?M_1), M37386. Pl. 15, fig. 10.

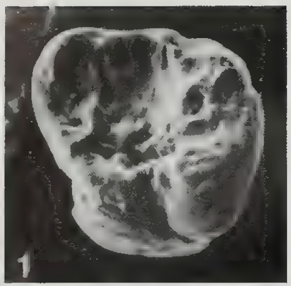
PARATYPES. (72): 7 DP^4 (M35532, M36101–4, M37366–7), 3 P^4 (M35539, M36099, M37365), 20 $M^{1/2}$ (M35533–5, M36038, M36105–13, M37368–73, M37699), 8 M^3 (M35537, M36054, M36115–7, M37374–6), 9 DP_4 (M36119–23, M37379–82), 3 P_4 (M36118, M37377–8), 19 $M_{1/2}$ (M35540–5, M36124–33, M37383–5), 3 M_3 (M36134–5, M37700).

DOUBTFULLY REFERRED MATERIAL. 20 upper incisors (M35579–81, M36136–41, M36175, M37387–95, M37701); lower incisor (M36142).

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Medium-sized species of *Sciuroides*, mean length of $M^{1/2}$ 2·68 mm. Lingual cusps of upper molars less than twice the height of the buccal cusps; height of buccal cusps of lower molars less than tooth width. Less than 25% of $M^{1/2}$s have metalophule I joining endoloph. 70% of $M_{1/2}$s lack enamel wrinkling. More than 85% of lower premolars and molars have oblique ectolophid which joins hypolophulid between a quarter and a third of the distance from the hypoconid.

DIFFERENTIAL DIAGNOSIS. *S. russelli* has stongly wrinkled molar enamel. Its lower premolar and molar ectolophids are bent in the middle, the mesial halves being oblique, the distal halves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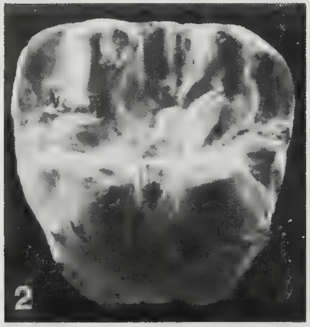
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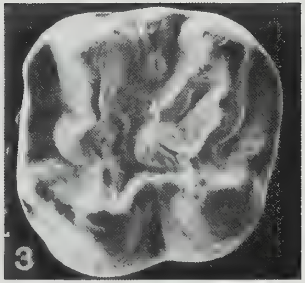
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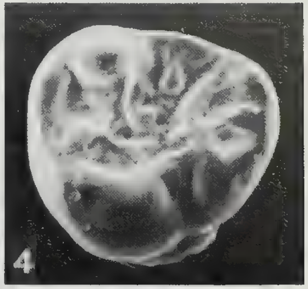
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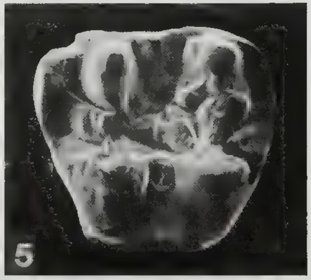
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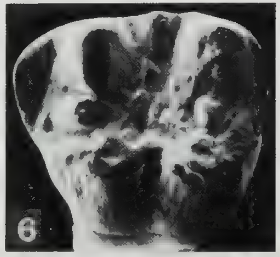
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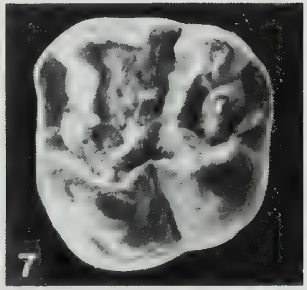
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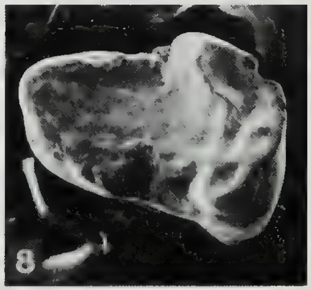
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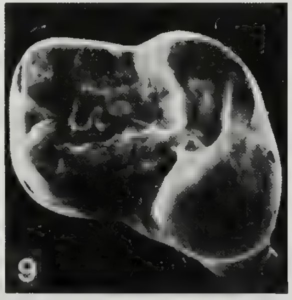
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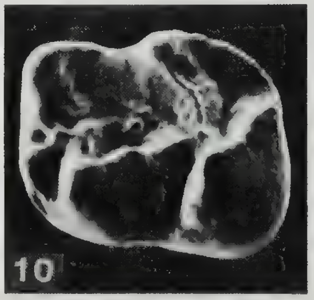
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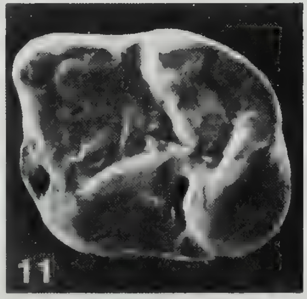
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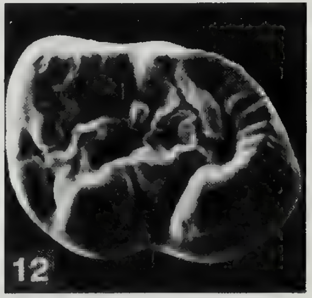
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Plate 15 Scanning electron micrographs of cheek teeth of *Sciuroides rissonei* sp. nov. from Creechbarrow, × 12·5. Fig. 1, right P^4 (reversed) (M36099). Fig. 2, left $M^{1/2}$ (M^1?) (M36106). Fig. 3, right $M^{1/2}$ (M^2?) (reversed) (M36111). Fig. 4, left M^3 (M37374). Fig. 5, left DP^4 (M35532). Fig. 6, right DP^4 (reversed) (M37367). Fig. 7, right $M^{1/2}$ (M^2?) (reversed) (M36107). Fig. 8, right DP_4 (reversed) (M37382). Fig. 9, left P_4 (M36118). Fig. 10, **holotype** right $M_{1/2}$ (M_1?) (reversed) (M37386). Fig. 11, left $M_{1/2}$ (M_2?) (M36128). Fig. 12, left M_3 (M36134). See p. 301.

Table 13 Statistics of length and width measurements of cheek teeth of *Sciuroides rissonei* from the Creechbarrow Limestone Formation, Creechbarrow. (N = number of specimens; OR = observed range; $\bar{x}$ = mean; s = standard deviation; v = coefficient of variation (in brackets where N is too few for v to be significant). See p. 194.

	Length					Width				
Tooth	N	OR	$\bar{x}$	s	v	N	OR	$\bar{x}$	s	v
DP^4	6	2·45–2·75	2·577	0·1203	4·67	7	2·20–2·75	2·414	0·1725	7·15
P^4	2	2·50–3·20	2·850	0·4949	(17·36)	3	2·60–3·00	2·767	0·2082	(7·52)
M$^{1/2}$	17	2·50–2·95	2·682	0·1030	3·84	17	2·65–3·10	2·806	0·1116	3·98
M^3	8	2·40–2·90	2·631	0·1438	5·47	8	2·30–2·90	2·531	0·1811	7·16
DP$_4$	7	2·45–2·75	2·521	0·1075	4·26	8	1·70–2·20	1·856	0·1568	8·45
P$_4$	3	2·80–2·95	2·867	0·0764	(2·67)	3	2·00–2·40	2·267	0·2309	(10·19)
M$_{1/2}$	16	2·55–2·90	2·775	0·1096	3·95	16	2·25–2·50	2·366	0·0831	3·51
M$_3$	2	3·20–3·25	3·225	0·0354	(1·10)	2	2·40–2·55	2·475	0·1061	(4·29)

(with the mesoconid) parallel with the buccal border of the tooth. The ectolophid joins the hypolophulid slightly nearer the hypoconid.

Note that Hartenberger & Louis (1976) recognized this species as congeneric with '*Suevosciurus romani*' but did not realize that both belong in the genus *Sciuroides*. Their diagnosis reflects this: '*Suevosciurus* légèrement plus petit que *S. mutabilis*. D4 et P4 inférieures et supérieures peu molarisées'. In fact *S. russelli* is slightly larger than the type assemblage of *Treposciurus mutabilis*, according to Schmidt-Kittler's (1971*a*: text-fig. 13) measurements.

S. ehrensteinensis is known from a small number of teeth from the English Headon Beds and the German fissure filling Ehrenstein 1A. It is slightly larger than *S. rissonei* or *S. russelli*, has higher lingual upper cheek tooth cusps and higher buccal and lingual lower cheek tooth cusps. Its metalophule I usually joins the endoloph (*fide* Bosma 1974: 33), and its ectolophids are bent.

S. siderolithicus is slightly smaller and has a bent ectolophid which joins the hypolophulid nearer the hypoconid.

DESCRIPTION. Close relationship between this species and *S. russelli* is reflected in the initial records from Creechbarrow (see synonymy list, p. 301). It is considered, however, that identification of *S. rissonei* as *S. russelli* on this basis would confuse, not clarify. The enamel wrinkling is an important specific character within the genus *Treposciurus* (see p. 308) and is thus also considered important in *Sciuroides*. The obliquity of the ectolophid is a notable primitive character within the family.

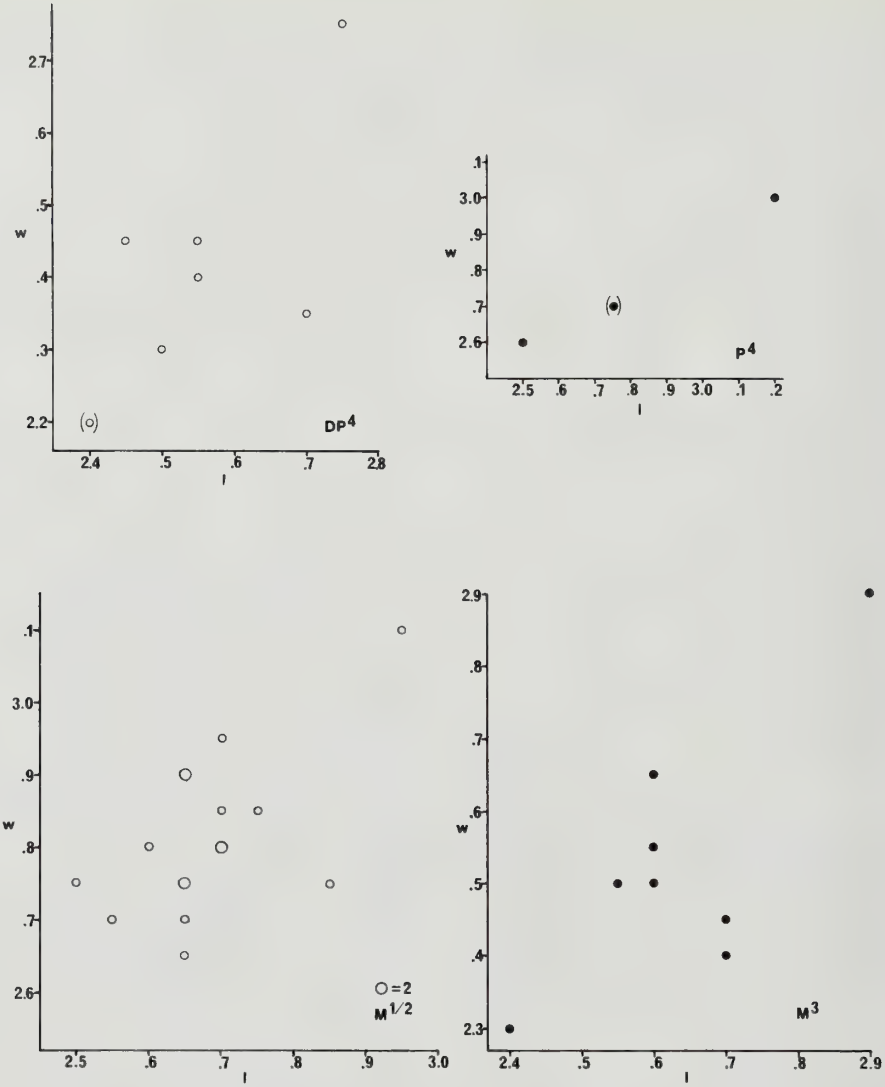
Tables 14–15 show percentage variation of characters for upper and lower cheek teeth. In addition, the paraconule is always large and the endoloph always complete on upper cheek teeth. Not all the incidences of characters are random. There is an 80% correlation between either one of metalophules I and II being broken and the other being complete in M$^{1/2}$. Fifteen specimens are involved. In one specimen (M37699) both I and II are almost broken. Two specimens (M36112 and M36038) have both I and II broken, but in addition have extra unnamed lophules. In M35535 metalophule II looks complete but is separated from the hypocone and joined to the lingual end of the posteroloph by a hypolophule. Pl. 15, figs 2–3 show metalophule I broken and metalophule II complete, while in fig. 7 the condition is reversed. Pl. 15, figs 5 and 6 show variations in shape and size of the parastyle in DP^4. Pl. 15, figs 10–11 show grade 1 enamel wrinkling, while fig. 12 shows grade 2 wrinkling. Unlike *S. ehrensteinensis* from the Isle of Wight (Bosma 1974: pl. 4, fig. 2) no mesostylids are present on any of the Creechbarrow teeth and only a faint ectostylid on one M$_3$. *S. russelli* M$_3$s sometimes have a crest joining the hypolophulid to the posterolophid; in *S. rissonei* there is one M$_1$ and one DP$_4$ where a projection distally from the hypolophulid fails to join the posterolophid. The interruption of the metalophulid is a good generic feature. There are two individual M$_{1/2}$s, however, where this crest is complete, but in both the anterolophulid is missing.

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Metalophule I joins lingually: metalophule II lingual to metaconule 2 (1), hypocone (2), distal endoloph (3) (7) (3) (8) (10) (0)	1	29	0	25	20	
	2	71	100	50	60	
	3	0	0	25	20	
Metalophule I broken/unbroken (7) (3) (7) (10) (0)	B	86	66·7	57	40	
	U	14	33·3	43	60	
Metalophule II broken/unbroken (7) (3) (6) (10) (6)	B	57	33·3	50	60	33·3
	U	43	66·7	50	40	66·7
Enamel wrinkling (0–3) (7) (3) (7) (10) (6)	0	100	0	100	50	33·3
	1	0	0	0	50	33·3
	2	0	33·3	0	0	33·3
	3	0	66·7	0	0	0
Mesostyle size (0–4) (7) (2) (8) (10) (6)	0	0	0	0	0	16·7
	1	0	0	0	0	0
	2	0	0	13	20	0
	3	86	100	25	80	33·3
	4	14	0	62	0	50
Mesostyle saliency: prominent (3), slight (2), non (1), ectoflexus (0) (7) (2) (5) (9) (7)	0	57	50	0	0	0
	1	43	50	40	22·2	43
	2	0	0	60	66·7	43
	3	0	0	0	11·1	14
Mesostyle mesiodistally elongated (7) (2) (4) (8) (5)	0	85·7	0	75	62·5	20
	1	14·3	100	25	37·5	80
Mesoloph length (0–3) (7) (3) (7) (9) (7)	0	0	0	0	0	14·2
	1	28·6	100	0	22·2	42·9
	2	57·1	0	100	77·8	42·9
	3	14·3	0	0	0	0
Protolophule I broken/unbroken (6) (3) (8) (10) (7)	B	16·7	66·7	0	30	28·6
	U	83·3	33·3	100	70	71·4
Metaconule 2 presence/absence (7) (2) (8) (9) (0)	0	0	50	0	0	
	1	100	50	100	100	
Hypolophule absent (0), partial (1), complete (2) (7) (2) (7) (9) (0)	0	85·7	0	85·7	66·7	
	1	14·3	50	14·3	22·2	
	2	0	50	0	11·1	
Posteroloph broken/unbroken lingually (7) (3) (7) (9) (0)	B	42·9	0	28·6	11·1	
	U	57·1	100	71·4	88·9	
Mesocone presence/absence (7) (3) (8) (10) (7)	0	85·7	100	50	100	57·1
	1	14·3	0	50	0	42·9
Sinus depth: shallow (1) to deep (4) (7) (3) (8) (10) (8)	1	0	0	0	0	0
	2	100	33·3	37·5	0	25·0
	3	0	66·7	25	80	62·5
	4	0	0	37·5	20	12·5
Protostyle presence/absence (6) (2) (7) (10) (8)	0	100	50	14·3	40	75
	1	0	50	85·7	60	25
Hypostyle presence/absence (7) (3) (8) (10) (0)	0	28·6	100	0	30	
	1	71·4	0	100	70	

Tables 14–15 Percentage character analysis of upper (Table 14) and lower (Table 15) cheek teeth of *Sciuroides rissonei* from Creechbarrow. 'Scoring units' give states for characters described in the left hand column. The numbers given under the tooth-headed columns on the right are percentages and refer to the number of teeth showing that particular character state. The lowest row of figures in the left hand column are the respective numbers of each tooth represented. See also p. 303.

Characters + (N) of representative teeth	Scoring units	DP_4	P_4	M_1	M_2	M_3
Distance along hypolophulid from hypoconid of junction with ectolophid (8) (3) (7) (10) (2)	$<\frac{1}{4}$	12·5	0	30	0	0
	$\frac{1}{4}$	50	0	70	30	100
	$\frac{1}{3}$	37·5	33·3	0	70	0
	$\frac{3}{8}$	0	33·3	0	0	0
	$\frac{3}{8}-\frac{1}{2}$	0	33·3	0	0	0
Orientation of ectolophid: straight oblique/bent parallel (7) (3) (7) (10) (2)	SO	43	100	57	90	100
	BP	57	0	43	10	0
Anteroconid size (1–3) (0) (0) (7) (10) (2)	1			30	40	0
	2			40	30	50
	3			30	30	50
Anterolophulid absent (0), weak (1), strong (2) (0) (0) (7) (10) (2)	0			15	23·3	50
	1			42	33·3	50
	2			43	43·3	0
Mesoconid length as % depth of sinusid (6) (3) (7) (10) (2)	0	0	66·7	0	0	0
	40	0	0	0	10	0
	50	33·3	33·3	29	10	50
	60	33·3	0	29	30	50
	70	33·3	0	21	15	0
	80	0	0	21	35	0
Mesolophid absent (0), $\frac{1}{4}$ complete (1), $\frac{1}{2}$ complete (2) (8) (3) (7) (10) (2)	0	60	100	70	40	0
	1	15	0	15	40	100
	2	25	0	15	20	0
Enamel wrinkling (0–2) (8) (3) (7) (10) (2)	0	85	0	57	70	50
	1	0	66·7	43	20	0
	2	15	33·3	0	10	50
Mesostylid presence/absence (8) (3) (7) (10) (2)	0	100	100	100	90	100
	1	0	0	0	10	0
Ectostylid presence/absence (8) (3) (7) (10) (2)	0	100	100	100	100	50
	1	0	0	0	0	50
Hypoconulid presence/absence (8) (3) (7) (10) (2)	0	15	33·3	57	60	50
	1	85	66·7	43	40	50
Distal crest to hypoconulid presence/absence (8) (3) (7) (10) (2)	0	87·5	100	14·3	100	100
	1	12·5	0	85·7	0	0

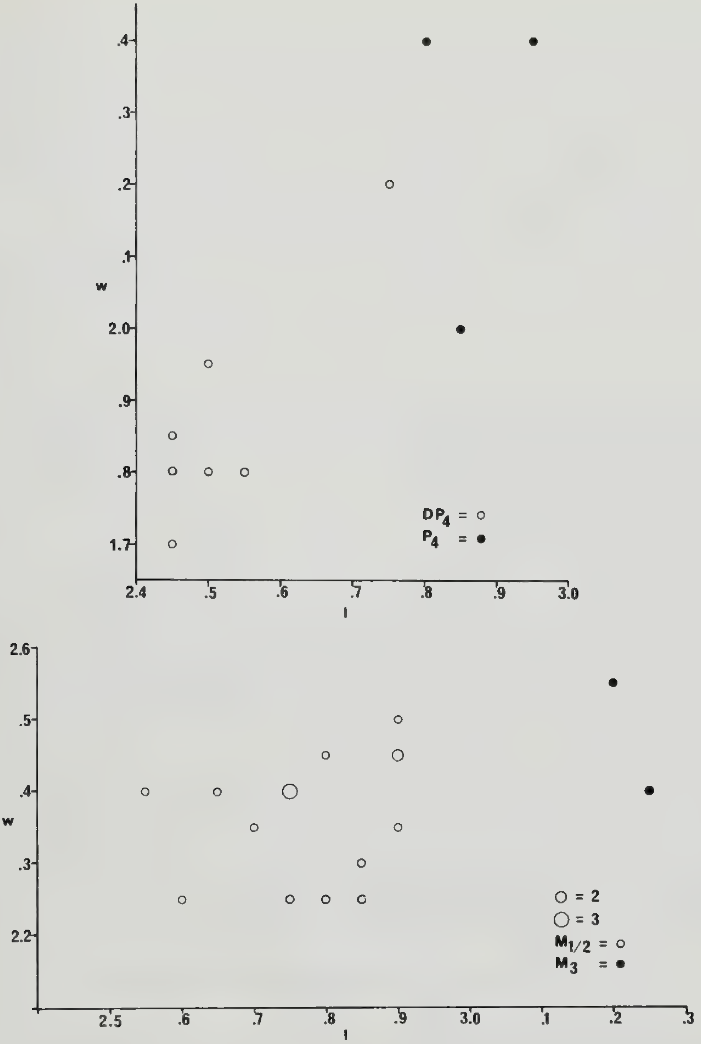
PHYLOGENETIC RELATIONSHIPS. Schmidt-Kittler (1971*a*) considered that there were three valid species of *Sciuroides*: *S. siderolithicus*, *S. ehrensteinensis* and *S.* sp. A. For him, *S. siderolithicus* gave rise to *S.* sp. A whereas *S. ehrensteinensis* was on a separate lineage. Bosma's (1974: 33) new material of *S. ehrensteinensis* indicated to her that *S.* sp. A fell within its range of variation.



Text-figure 32 Scatter diagrams of length (l) against width (w) in DP^4, P^4, M$^{1/2}$ and M^3 of *Sciuroides rissonei* sp. nov. from Creechbarrow. Measurements in millimetres.

Subsequently the discoveries of *S. russelli* and *S. rissonei* from the Bartonian provide more potential candidates for the ancestry of *S. ehrensteinensis*. In the sum of its characters, *S. rissonei* is the most primitive species of *Sciuroides* and could have given rise to all the others. It is easy to envisage the small changes needed for it to give rise to both *S. russelli* and *S. siderolithicus*; and specimens intermediate in size between *S. siderolithicus* and *S. ehrensteinensis* from Eclépens B and Weidenstetten (*S.* aff. *siderolithicus* of Schmidt-Kittler 1971*a*) give an idea of the probable origin of *S. ehrensteinensis*.

Two important generic characters of *Sciuroides*, the high endoloph and the incomplete metalophulid, are shared with *Protadelomys lugdunensis* from the Auversian of Lissieu. One important character of *P. lugdunensis* is shared with *Sciuroides rissonei*: the oblique ectolophid.



Text-figure 33 Scatter diagrams of length (l) against width (w) in DP$_4$, P$_4$, M$_{1/2}$ and M$_3$ of *Sciuroides rissonei* sp. nov. from Creechbarrow. Measurements in millimetres.

This makes *P. lugdunensis* the best candidate we have for ancestry of the genus *Sciuroides*. The probable mode of development of metalophule I is described above under Pseudosciuridae (p. 299).

Genus *TREPOSCIURUS* Schmidt-Kittler 1970

TYPE SPECIES. *T. mutabilis* Schmidt-Kittler 1970. Ludian fissure filling; Ehrenstein 1A, near Ulm, West Germany.

INCLUDED SPECIES. *T. intermedius* (Schlosser 1884) Schmidt-Kittler 1970, *T. helveticus* Schmidt-Kittler 1971*a*, new rank.

RANGE. Marinesian–Ludian; England, France, Spain, Switzerland and West Germany.

Emended diagnosis. Upper cheek teeth with: endoloph low, usually incomplete; metalophule I strong to weak, not dentine-cored (except sometimes at metaconule 1), complete, incomplete or missing, and in M^{1-2} attached to endoloph from near middle to near hypocone; paraconule weak on P^4, strong on DP^4 and $M^{1\ 2}$, may be weak on M^3; metaconule 2 present or absent. DP^4 with medium-sized, often bicuspid parastyle and straight mesiolingual margin. Lower cheek teeth with: ectolophid low, complete to incomplete, bent parallel, joining hypolophulid between hypoconid and one-third of the distance from the hypoconid to the entoconid; mesoconid weak to strong. Lower molars with: M_{1-2} anteroconid absent to large, usually buccal to midline; anterolophulid present or absent; anterolophid strong; metalophulid high and complete to low and incomplete. M_3 hypolophulid high to low, usually complete. DP_4 with: crown height lower than that of molars; metalophulid present to absent. Anterior palatine foramina project just posterior to maxillary–premaxillary suture (known for *T. mutabilis* and *T. intermedius*).

Treposciurus helveticus Schmidt-Kittler 1971*a*, new rank

v* 1971*a* *Treposciurus mutabilis helveticus* Schmidt-Kittler: 53–57; pl. 2, fig. 7; text-figs 23–24.
v. *1977b* *Treposciurus* sp.; Hooker: 141.
v. *1980* *Treposciurus* sp.; Hooker & Insole: 39.

Types. See under nominate subspecies.

Range. Marinesian to early Ludian; England and Switzerland.

Emended diagnosis. M^{1-2} metalophule I not dentine-cored, incomplete to complete, joining endoloph just distal to sinus (at mesocone if present) or nearer hypocone, or may be absent sometimes replaced by fairly strong enamel wrinkling. M_{1-2} with weak enamel wrinkling or just a few strong folds; moderately to strongly developed anteroconid with weak or no anterolophulid and moderate anterolophid; mesoconid usually strong, tending to extend more than half the depth of the sinusid. DP_4 lacks metalophulid.

Differential diagnosis. *T. mutabilis*: all cheek teeth possess strong reticulate enamel. M^{1-2} consistently lack any metalophule I. M_{1-2} anteroconid is weak to absent, anterolophulid usually present, anterolophid strong; mesoconid usually weak but often extending as narrow ridge through the sinusid. DP_4 has metalophulid.

T. intermedius: $M^{1\ 2}$ consistently possess incomplete to complete metalophule I, joining endoloph at or near hypocone. M_{1-2} mesoconid usually weak.

Treposciurus helveticus helveticus Schmidt-Kittler 1971*a*

v* 1971*a* *Treposciurus mutabilis helveticus* Schmidt-Kittler: 53–57; pl. 2, fig. 7; text-figs 23–24.
v. 1971*a* *Pseudosciurus* A n. sp.; Schmidt-Kittler: 29, text-fig. 9.

Table 16 Statistics of length and width measurements of cheek teeth of *Treposciurus helveticus preecei* from Creechbarrow. (Notation as in Table 13, p. 303).

Tooth	Length					Width				
	N	OR	$\bar{x}$	s	v	N	OR	$\bar{x}$	s	v
DP^4	3	2·10–2·27	2·18	0·0854	(3·92)	5	1·87–2·10	1·99	0·1031	5·17
P^4	2	1·77–2·05	1·91	0·1980	(10·37)	2	1·88–2·03	1·96	0·1061	(5·41)
$M^{1/2}$	18	1·95–2·25	2·10	0·0834	3·98	19	1·98–2·28	2·15	0·0946	4·39
M^3	6	1·85–2·13	2·05	0·0972	4·75	5	1·83–2·21	2·06	0·1462	7·10
DP_4	1	1·82	–	–	–	1	1·33	–	–	–
P_4	4	1·93–2·10	2·01	0·0850	(4·23)	4	1·58–1·89	1·72	0·1365	(7·94)
$M_{1/2}$	14	2·05–2·40	2·18	0·0996	4·57	12	1·73–2·10	1·93	0·1093	5·66
M_3	7	2·33–2·71	2·48	0·1337	5·40	7	1·81–2·00	1·91	0·0628	3·28

TYPES AND RANGE. Holotype (LGM 40209) and paratypes from the Sidérolithique, Eclépens (B?), Canton Vaud, Switzerland; teeth in the NMB (referred herein) also from Eclépens B. Schmidt-Kittler (1971*a*: 53–57) only recorded his material as being from Eclépens, but all rodent material from the new fissures was collected from Eclépens B (personal communication, D. Rigassi 1980).

EMENDED DIAGNOSIS. Mean length of $M^{1/2}$ 2·33 mm. Range 2·08–2·64 mm.

Treposciurus helveticus preecei subsp. nov.
(Pl. 16; Pl. 17, figs 1–6; Text-figs 34–35; Tables 16–18)

v. *1977b* *Treposciurus* sp.; Hooker: 141.
v. *1980* *Treposciurus* sp.; Hooker & Insole: 39.

NAME. After Dr R. Preece for help with field work.

TYPES. As the definition of this subspecies is based on a size range which overlaps with the other subspecies, and as its morphological variation is very high, the designation of a holotype is inappropriate. Therefore contrary to Recommendation 73A of the International Code of Zoological Nomenclature (1985: 149), I give all members of this type series equal status in the form of 75 **syntypes**: 6 DP^4 (M36034–7, M36100, M37331), 4 P^4 (M36032–3, M37330, M37337), 25 $M^{1/2}$ (M35509–10, M35512–4, M36039, M36041–53, M36067, M37332–6), 7 M^3 (M35515–8, M36055, M37338–9), 1 DP_4 (M36058), 6 P_4 (M35538, M36056–7, M37340–2), 19 $M_{1/2}$ (M35519–29, M36059–60, M36062–3, M37343–6), 7 M_3 (M35530–1, M36064–6, M37347–8).

DOUBTFULLY REFERRED MATERIAL. 53 upper incisors (M35564–73, M36068–96, M36170–4, M37349–57); 14 lower incisors (M35574–8, M36097–8, M37358–64).

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

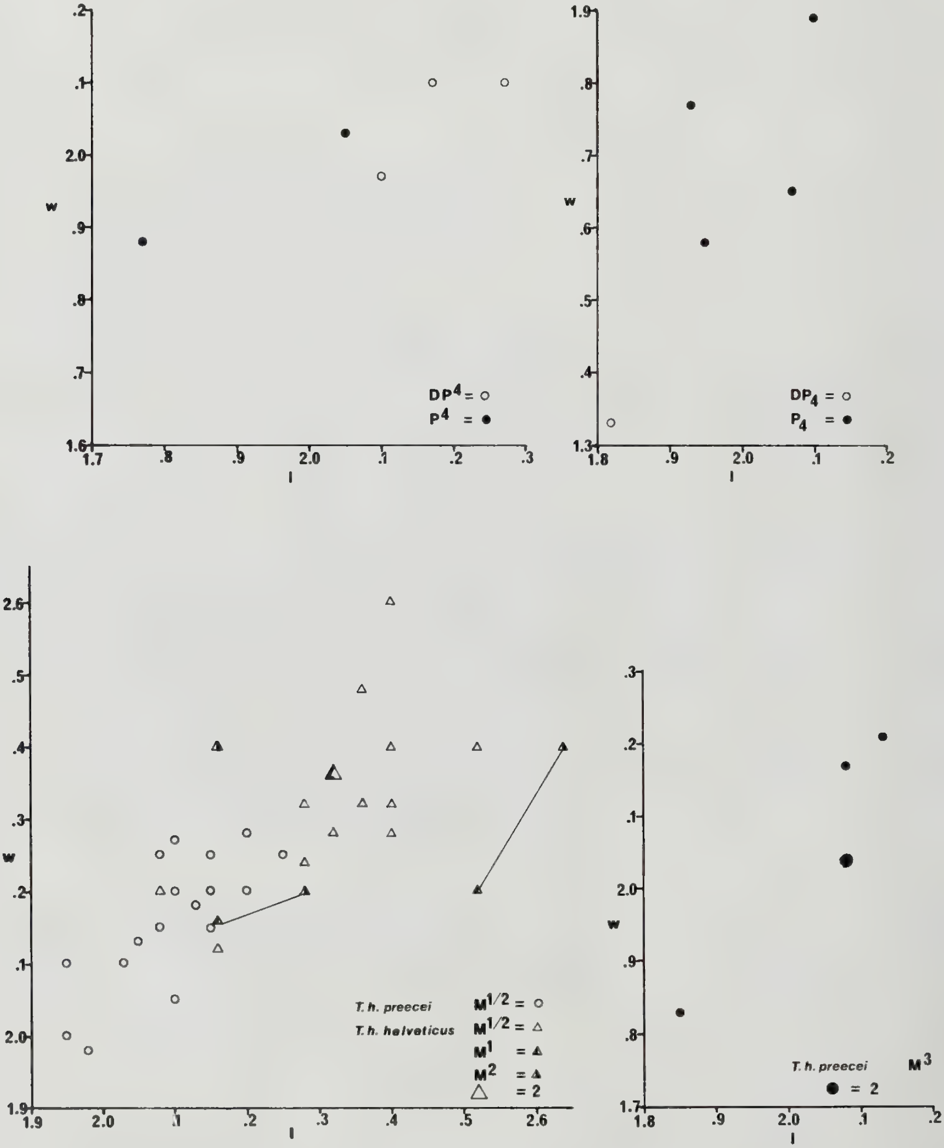
DIAGNOSIS. Mean length of $M^{1/2}$ 2·10 mm. Range 1·95–2·25 mm.

COMMENT ON TAXONOMY. The *Treposciurus* from Creechbarrow is very similar in morphology and range of morphological variation to the type and referred material of *T. mutabilis helveticus* from Eclépens B. The only tangible difference is in the size, it being smaller but with overlapping range. As there are morphological differences between *T. m. helveticus* and *T. m. mutabilis*, especially now that the former is known from more material from the type locality, it is proposed here that the subspecies *T. m. helveticus* be raised to the rank of species.

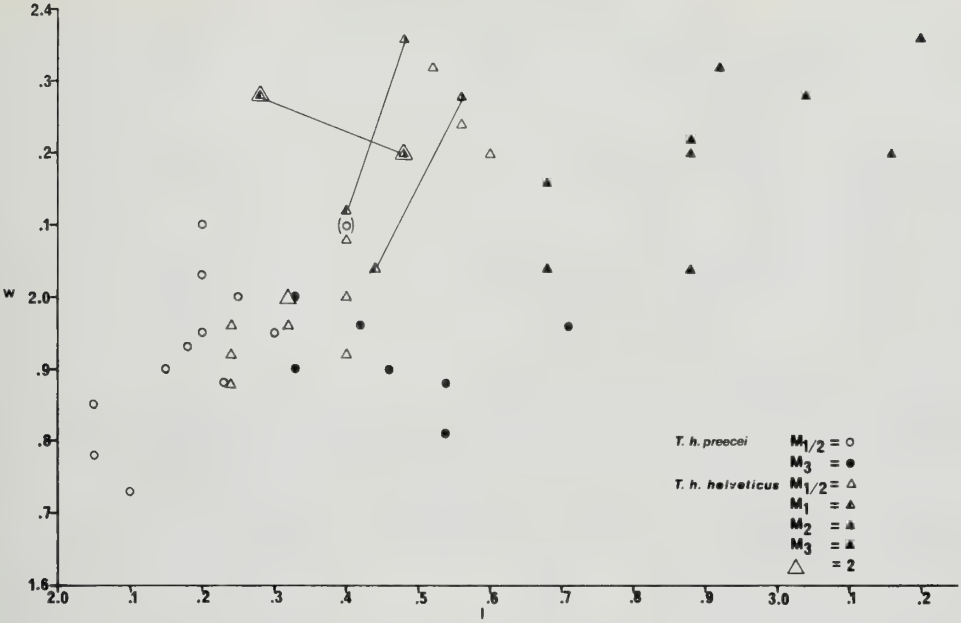
Material from the Headon and Osborne Beds, referred by Bosma (1974) and Bosma & Insole (1976) to *T. m. helveticus*, is morphologically very similar to *T. m. mutabilis*. It differs only in being slightly smaller, but there is much overlap in measurements. Therefore it is proposed to refer this material to *T. mutabilis* with no division into subspecies. The overlap in size between the Creechbarrow *Treposciurus* and *T. helveticus* Schmidt-Kittler 1971*a*, new rank, from Eclépens B is much less and it is proposed to recognize them as conspecific but belonging to different subspecies.

DESCRIPTION. Of the three English Bartonian pseudosciurids, *T. helveticus preecei* is the most variable in morphology, especially in the upper molars. Since two particular morphologies, which characterize respectively *T. mutabilis* and *T. intermedius*, are present at Creechbarrow, it could be doubted that only a single species were represented there. However, the lack of any clear-cut morphological differences on which subdivisions could be made, the unimodal size distribution and its low coefficient of variation (Table 16) especially in the first and second molars, and the presence of similar morphological range in the Eclépens B assemblage of *T. helveticus*, serve to remove doubt.

In Tables 17–18, morphological variation is given as in Tables 20–21 for *Suevosciurus authodon* (pp. 319–321). The major variations in $M^{1/2}$ are illustrated in Pl. 16, figs 2–3, 7, 9–12. Pl. 16, fig. 11 shows a morphology almost identical to that of *T. mutabilis*; the only difference is that the enamel in the centre of the tooth is not quite so strongly or deeply reticulate as is usual for *T. mutabilis*. Fig. 12 shows a morphology almost identical to that of *T. intermedius*; the replacement of the lingual end of metalophule II by a hypolophule joining the posteroloph is a variant feature which can often occur in any species of *Treposciurus* or *Suevosciurus.* The former tooth is the largest in the assemblage and the latter one of the smallest, thus corresponding to the respective size differences of the Ludian species they resemble. Apart from these extremes there are specimens that show a mainly incomplete metalophule I which usually joins the endoloph just distal to the midpoint, unlike *T. intermedius* where it joins the endoloph



Text-figure 34 Scatter diagrams of length (l) against width (w) in DP^4, P^4, DP$_4$ and P$_4$ of *Treposciurus helveticus preecei* subsp. nov. from Creechbarrow, and in M$^{1/2}$ of *Treposciurus helveticus helveticus* Schmidt-Kittler from Eclépens B and M$^{1/2}$ and M^3 of *T. helveticus preecei* from Creechbarrow. Measurements in millimetres. Lines join teeth of one individual.



Text-figure 35 Scatter diagrams of length (l) against width (w) in $M_{1/2}$ and M_3 of *Treposciurus helveticus helveticus* Schmidt-Kittler from Eclépens B and *T. helveticus preecei* subsp. nov. from Creechbarrow. Measurements in millimetres. Lines join teeth of one individual.

nearer the hypocone. Some specimens have smooth enamel and no metalophule I at all and there are complex intermediates between most of these types. Fig. 7 shows a doubled metaconule 2, whilst Fig. 9 shows a single, huge, undivided metaconule such as occurs in the late Lutetian *Protadelomys cartieri* from Egerkingen γ, Switzerland. One very curious $M^{1/2}$ (M35514) is relatively elongated, has no metalophule I, a very shallow sinus and a strong lingual cingulum completely spanning the sinus and rising distally to about a third the crown height of the hypocone.

There is less variation in the lower molars. No $M_{1/2}$s show features typical of *T. mutabilis* and the lower molars of *T. intermedius* have no special distinguishing characters. M35524 is peculiar in having a double mesoconid. An M_3 (M37348) deserves special mention (Pl. 17, fig. 6); unlike the typical shape shown in Pl. 17, fig. 4, its outline is a parallelogram, the acute angles being the mesiolingual and distobuccal corners.

PHYLOGENETIC RELATIONSHIPS. From the polymorphic pattern described above it is possible to formulate a phylogenetic model for the three *Treposciurus* species. This involves a cladogenesis with *T. helveticus* as the common ancestor of *T. mutabilis* and *T. intermedius*. The two Ludian species would have developed by selection of different morphs already present in the Bartonian species. The two daughter species are thus more specialized than the ancestral species. This speciation event seems to have occurred at about the Bartonian/Ludian boundary, at a time when there was a widespread marine regression with mammalian migrations and extinctions within Europe (see Garimond *et al.* 1975), thus increasing selection pressures.

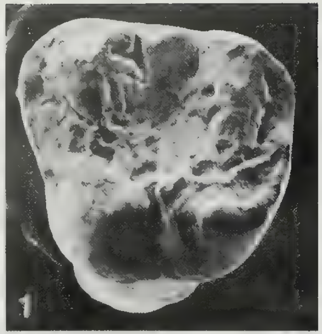
It is not certain whether the differences between the two subspecies of *T. helveticus* reflect geographical or stratigraphical separation. There is some biostratigraphical evidence that Eclépens B is younger than Creechbarrow (see correlation section, pp. 425–427). Alternatively, if the subspecies were geographical, it is possible that *T. intermedius* arose in the region of southern England and *T. mutabilis* in the region of Switzerland.

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Metalophule I joins lingually: metalophule II lingual to metaconule 2 (1), hypocone (2), distal endoloph (3), central endoloph (4); is absent (0) (5) (4) (8) (11) (0)	0	0	75	37·5	63·6	
	1	20	0	0	0	
	2	80	25	12·5	9·1	
	3	0	0	0	18·2	
	4	0	0	50·0	9·1	
Metalophule I broken/unbroken (5) (4) (8) (11) (0)	B	60	100	100	90·9	
	U	40	0	0	9·1	
Metalophule II broken/unbroken (5) (4) (8) (11) (4)	B	0	25	50	18·2	75
	U	100	75	50	81·8	25
Enamel wrinkling (0–3) (6) (3) (7) (8) (6)	0	83·3	0	0	12·5	0
	1	0	0	85·7	50·0	0
	2	16·7	33·3	14·3	37·5	0
	3	0	66·7	0	0	100
Mesostyle size (0–4) (5) (3) (7) (11) (5)	0	0	0	0	0	80
	1	0	0	0	0	0
	2	0	66·7	0	9·1	0
	3	80	33·3	100	90·9	0
	4	20	0	0	0	20
Mesostyle saliency: slight (2), non (1), ectoflexus (0) (4) (3) (7) (10) (5)	0	25	0	0	0	0
	1	50	66·7	85·7	100	40
	2	25	33·3	14·3	0	60
Mesostyle mesiodistally elongated (5) (3) (8) (11) (5)	0	100	100	87·5	100	0
	1	0	0	12·5	0	100
Mesoloph length (0–3) (5) (3) (8) (11) (5)	0	20	33·3	25	27·2	100
	1	40	66·7	12·5	18·2	0
	2	20	0	50	45·5	0
	3	20	0	12·5	9·1	0
Protolophule I broken/unbroken (5) (3) (8) (8) (5)	B	0	66·7	75	37·5	20
	U	100	33·3	25	62·5	80
Metaconule 2 presence/absence (6) (3) (8) (10) (0)	0	33·3	0	12·5	80	
	1	66·7	100	87·5	20	
Hypolophule absent (0), partial (1), complete (2) (6) (3) (8) (10) (0)	0	100	100	87·5	90	
	1	0	0	0	0	
	2	0	0	12·5	10	
Posteroloph broken/unbroken lingually (4) (4) (8) (9) (0)	B	50	0	87·5	44·4	
	U	50	100	12·5	55·6	
Mesocone presence/absence (6) (4) (8) (10) (7)	0	100	100	62·5	80	57·1
	1	0	0	37·5	20	42·9
Sinus depth: shallow (1) to deep (4) (5) (4) (8) (10) (7)	1	0	0	12·5	0	0
	2	20	75	37·5	20	14·3
	3	80	25	37·5	50	57·1
	4	0	0	12·5	30	28·6
Protostyle presence/absence (5) (3) (8) (11) (4)	0	20	66·7	62·5	36·4	50
	1	80	33·3	37·5	63·6	50

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Hypostyle presence/absence	0	25	100	25	60	
(4) (4) (8) (10) (0)	1	75	0	75	40	
Paraconule small (1), large (2)	1	0	33·3	0	0	28·6
(6) (3) (8) (11) (7)	2	100	66·7	100	100	71·4
Endoloph broken (1), complete (2)	1	0	25	50	12·5	0
(6) (4) (8) (9) (5)	2	100	75	50	87·5	100
DP^4 parastyle bicuspid	0	66·7				
(3)	1	33·3				

Tables 17–18 Percentage character analysis of upper (opposite and above) and lower (below) cheek teeth of *Treposciurus helveticus preecei* from Creechbarrow. For explanation see Table 14, p. 305.

Characters + (N) of respective teeth	Scoring units	DP$_4$	P$_4$	M$_1$	M$_2$	M$_3$
Distance along hypolophulid	$<\frac{1}{4}$	100	25	45·4	50	83·3
from hypoconid of junction	$\frac{1}{4}$	0	75	36·4	50	16·7
with ectolophid	$\frac{1}{3}$	0	0	18·2	0	0
(1) (4) (11) (6) (6)						
Anteroconid size (1–3)	1			40	33·3	50
(0) (0) (10) (6) (6)	2			40	66·7	50
	3			20	0	0
Anterolophulid absent (0), weak	0			87·5	83·3	80
(1), strong (2)	1			12·5	16·7	0
(0) (0) (8) (6) (5)	2			0	0	20
Mesoconid length as % depth of	40	100	0	0	0	0
sinusid	50	0	0	10	0	0
(1) (4) (10) (6) (6)	60	0	0	0	33·3	0
	70	0	25	30	33·3	16·7
	80	0	75	40	16·7	16·7
	90	0	0	10	16·7	66·6
	100	0	0	10	0	0
Mesolophid absent (0), $\frac{1}{4}$ complete (1)	0	100	25	45·5	66·7	50
(1) (4) (11) (6) (6)	1	0	75	54·5	33·3	50
Enamel wrinkling (0–2)	0	100	0	75·0	80	0
(1) (4) (8) (5) (6)	1	0	25	12·5	20	50
	2	0	75	12·5	0	50
Mesostylid presence/absence	0	100	100	70	60	83·3
(1) (4) (10) (5) (6)	1	0	0	30	40	16·7
Ectostylid presence/absence	0	100	100	100	83·3	100
(1) (4) (8) (6) (6)	1	0	0	0	16·7	0
Hypoconulid presence/absence	0	0	50	70	60	66·7
(1) (4) (10) (5) (6)	1	100	50	30	40	33·3
Distal crest to hypolophulid	0	100	100	90·9	100	100
(1) (4) (11) (6) (6)	1	0	0	9·1	0	0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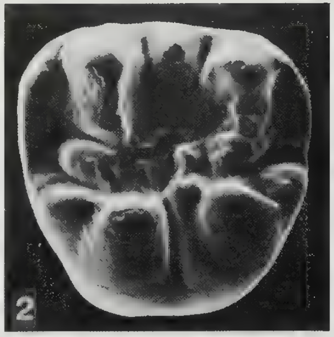
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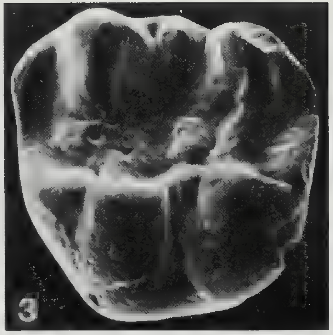
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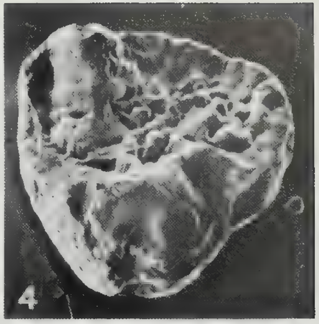
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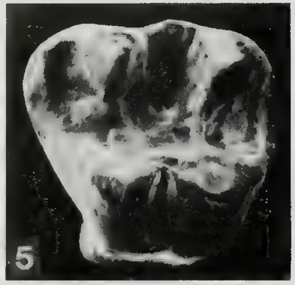
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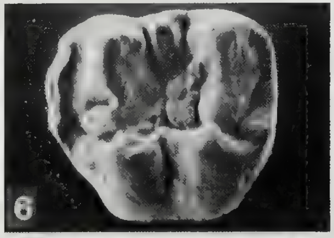
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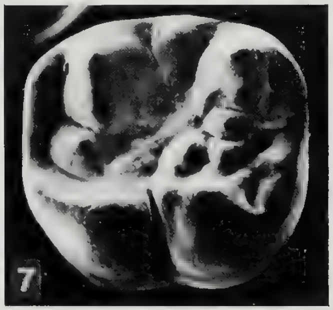
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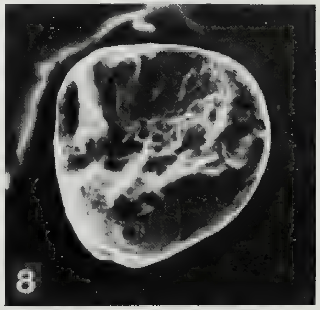
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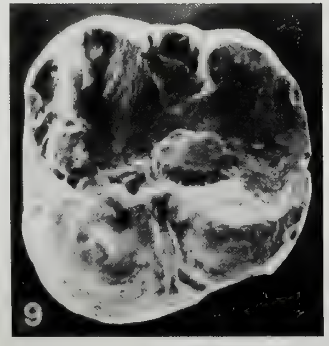
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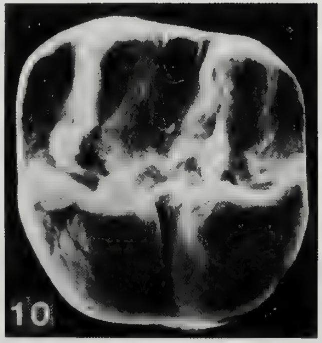
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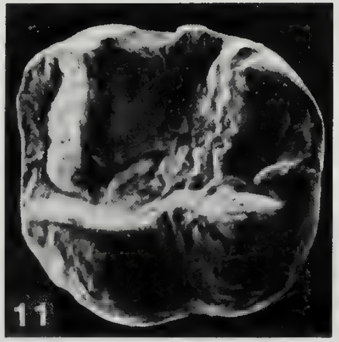
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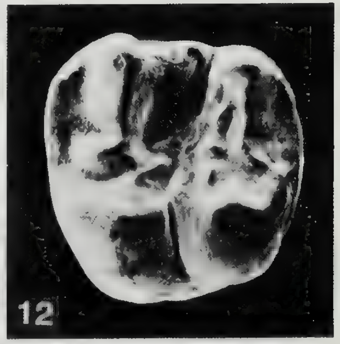
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Genus *SUEVOSCIURUS* Dehm 1937
[incl. *Suevosciurus* (*Microsuevosciurus*) Hartenberger, 1973]

TYPE SPECIES. *Sciuroides fraasi* Major 1873. Ludian fissure filling; Örlinger Tal, West Germany.

INCLUDED SPECIES. *S. ehingensis* Dehm 1937, *S. minimus* (Major 1873), *S. palustris* (Misonne 1957) and *S. authodon* sp. nov. Note that Bosma (1974: 53) has removed Hartenberger's (1973: pl. 1, figs 6–13) '*Suevosciurus* aff. *minimus*' from Fons 4 from *Suevosciurus* and compared it with *Treposciurus*.

RANGE. Marinesian–Ludian, England; Ludian–Stampian, W. Germany; Ludian, France and Switzerland; early Stampian, Belgium; Oligocene, Majorca.

EMENDED DIAGNOSIS. Upper cheek teeth with: endoloph high, usually complete; M^{1-2} metalophule I usually missing, occasionally present, not dentine-cored, developed as ridge lingually only or as metaconule 1, in which case usually attached to endoloph just distal to midpoint; paraconule strong to weak on DP^4 and M^{1-3}; metaconule 2 usually absent; DP^4 with medium to large, often bicuspid parastyle and usually concave mesiolingual margin. Lower cheek teeth with: ectolophid complete, but low, to incomplete, bent parallel, joining hypolophulid at or close to hypoconid; mesoconid nearly always strong. Lower molars with: M_{1-2} anteroconid usually large, usually buccal to midline: anterolophulid nearly always absent; anterolophid strong; metalophulid high and complete. M_3 hypolophulid incomplete or low and complete. $DP\frac{4}{4}$ with: crown height equal to that of molars; metalophulid present. Anterior palatine foramina project just posterior to maxillary–premaxillary suture (known for *S. fraasi* and *S. ehingensis*).

PREVIOUS DIAGNOSES. The most recent was by Hartenberger (1973: 11), but this reflects his inclusion in the genus of species referable to *Treposciurus* and *Sciuroides* (see discussions under these genera). The diagnosis herein is closer to that of Schmidt-Kittler (1971*a*: 39) but involves the reidentification of his $P\frac{4}{4}$ as $DP\frac{4}{4}$ and the characters of subsequently described material from the Isle of Wight (Bosma 1974) and Creechbarrow (herein).

Suevosciurus authodon sp. nov.
(Pl. 17, figs 7–12; Pl. 18; Text-figs 36–39; Tables 19–21)

v. *1977b* *Suevosciurus* sp.; Hooker: 141.
v. *1980* *Suevosciurus* sp. 1; Hooker & Insole: 39.

NAME. Noun in apposition, from Greek *αὖθις*, afresh, and *ὀδούς*, tooth, in allusion to the tooth replacement in this species.

HOLOTYPE. Right DP^4, M35469. Pl. 18, fig. 5.

PARATYPES. (336): 27 DP^4 (M35470–1, M35787, M35797–813, M36447, M37205–10); 23 P^4 (M35464–8, M35486, M35785–6, M35788–96, M37199–204); 102 $M^{1/2}$ (M35472–7, M35814–75, M37211–35); 25 M^3 (M35488–90, M35876–88, M37236–44): 2 DP_4 (M35897, M37247); 13 P_4 (M35491–2, M35889–96, M35898, M37245–6); 102 $M_{1/2}$ (M35493–504, M35899–960, M37248–75); 42 M_3 (M35505–8, M35961–87, M37276–86).

DOUBTFULLY REFERRED MATERIAL. 44 upper incisors (M35549–53, M35988–36008, M36161–2, M37287–302); 67 lower incisors (M35554–63, M36009–31, M36163–9, M37303–29).

Plate 16 Scanning electron micrographs of upper cheek teeth of *Treposciurus helveticus preecei* subsp. nov. from Creechbarrow, × 18. All are **syntypes**. Fig. 1, left P^4 (M36032). Fig. 2, left $M^{1/2}$ (M^1?) (M36045). Fig. 3, left $M^{1/2}$ (M^2?) (M36043). Fig. 4, left M^3 (M35516). Fig. 5, left DP^4 (M36100). Fig. 6, right DP^4 (reversed) (M36037). Fig. 7, right $M^{1/2}$ (M^1?) (reversed) (M35513). Fig. 8, right M^3 (reversed) (M35518). Fig. 9, right $M^{1/2}$ (M^2?) (reversed) (M35512). Fig. 10, right $M^{1/2}$ (M^2?) (reversed) (M37334). Fig. 11, right $M^{1/2}$ (M^2?) (reversed) (M36051). Fig. 12, left $M^{1/2}$ (M^2?) (M36039). See p. 309.

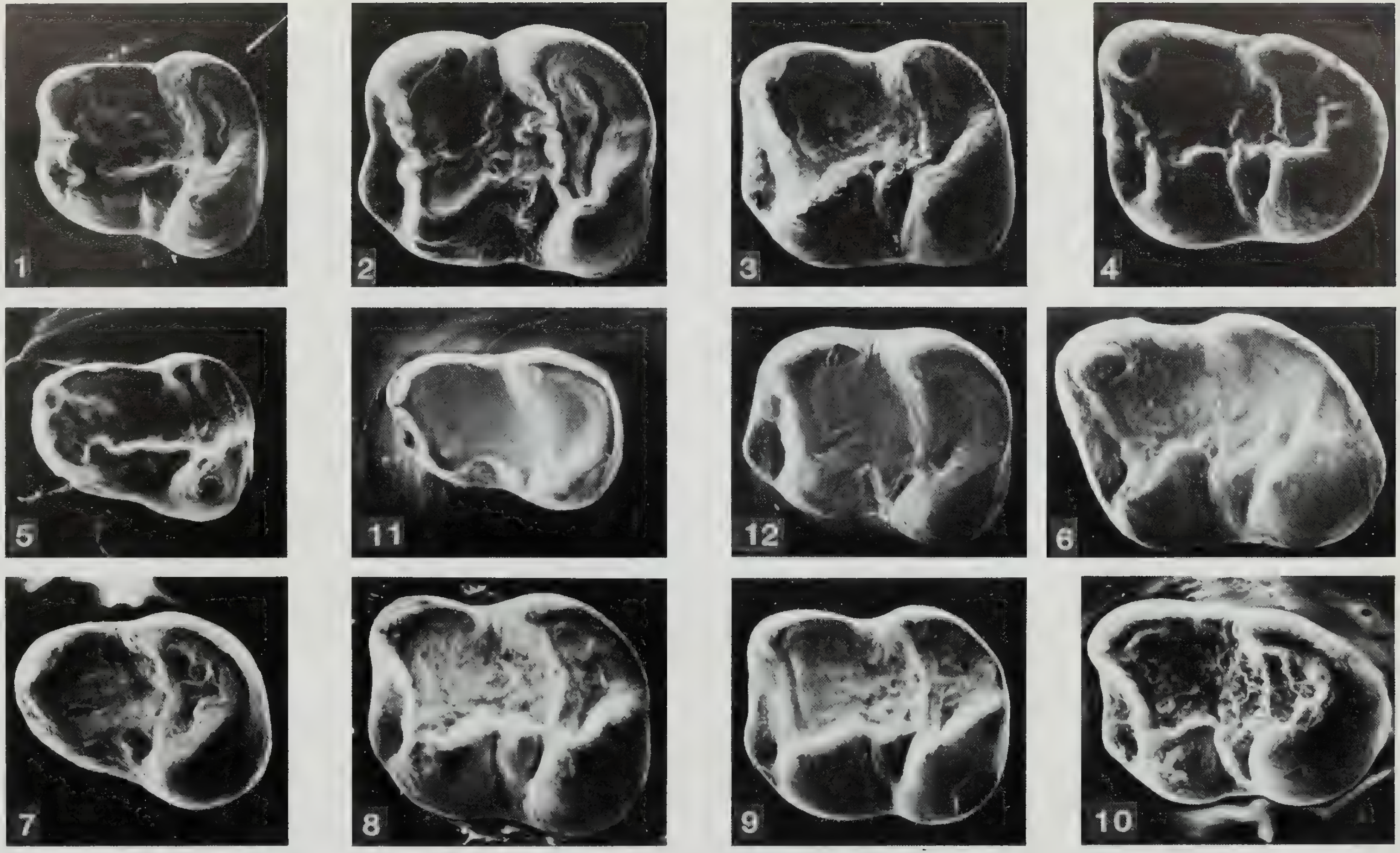


Plate 17 Scanning electron micrographs of lower cheek teeth of *Treposciurus* and *Suevosciurus* from Creechbarrow.

Figs 1–6 *Treposciurus helveticus preecei* subsp. nov., **syntypes**, × 18. Fig. 1, right P_4 (reversed) (M37342). Fig. 2, right $M_{1/2}$ (M_1?) (reversed) (M37346). Fig. 3, right $M_{1/2}$ (M_2?) (reversed) (M37345). Fig. 4, right M_3 (reversed) (M36065). Fig. 5, left DP_4 (M36058). Fig. 6, right M_3 (reversed) (M37348). See p. 309.

Figs 7–12 *Suevosciurus authodon* sp. nov., × 25. Fig. 7, left P_4 (M35891). Fig. 8, left $M_{1/2}$ (M_1?) (M35918). Fig. 9, right $M_{1/2}$ (M_2?) (reversed) (M35926). Fig. 10, left M_3 (M35961). Fig. 11, right DP_4 (reversed) (M35897). Fig. 12, left $M_{1/2}$ (M_1?)(M35907). See p. 315.

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Mean length of $M^{1/2}$ 1·49 mm; range 1·350–1·625 mm. P^4_4 present. DP^4 mean length/width ratio 1·08. 70% $M^{1/2}$s have size 2 metaconule 1.

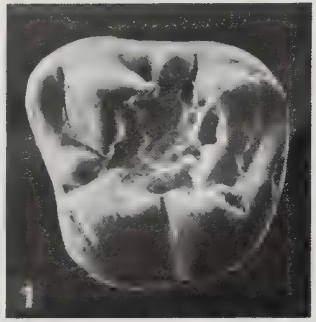
DESCRIPTION. One of the most important discoveries in the Creechbarrow material is of upper and lower fourth permanent premolars. Teeth previously identified as such can now be conclusively identified as upper and lower fourth deciduous premolars. The possibility of DP4 retention in *Suevosciurus* was first suggested by Bosma (1974: 40). She reasoned that no distinction could be made between deciduous and permanent premolars despite the abundant material available and that 'P^4' had a strong parastyle typical of DP^4 in other pseudosciurid genera. The supposed characters of 'P^4' can no longer be used as a constant diagnostic feature for *Suevosciurus* and even though retention of DP^4_4 characterizes the best-known of the various species, it cannot be used in the generic diagnosis with the inclusion of *S. authodon*. Nevertheless the increase in crown height of DP^4_4 can be used and this probably foreshadowed later loss of P^4_4.

There is much variation in practically all the known morphological characters of *Suevosciurus* and size has been used by previous workers almost exclusively to distinguish between species. The low coefficients of variation for the large tooth assemblage from Creechbarrow indicate the presence of a single species (Table 19). An attempt is made here to provide numerical scales for features of variable size (e.g. mesostyle), or just to indicate presence or absence, and to show percentage occurrence within the Creechbarrow assemblage (see Tables 20–21). It is hoped that this will encourage other workers to do the same for their material, to allow species-level distinctions on at least percentage characters. Some are suggested under Phylogenetic Relationships (p. 321).

Table 19 Statistics of length and width measurements of cheek teeth of *Suevosciurus authodon* from Creechbarrow. (Notation as in Table 13, p. 303).

Tooth	Length					Width				
	N	OR	x̄	s	v	N	OR	x̄	s	v
DP^4	17	1·250–1·550	1·43	0·086	6·00	23	1·150–1·625	1·34	0·099	7·38
P^4	21	1·375–1·625	1·49	0·075	5·06	22	1·350–1·550	1·45	0·066	4·58
$M^{1/2}$	84	1·350–1·625	1·49	0·055	3·71	86	1·375–1·675	1·57	0·068	4·36
M^3	24	1·250–1·500	1·38	0·059	4·25	23	1·325–1·525	1·42	0·053	3·73
DP_4	2	1·350–1·400	1·38	0·035	(2·57)	2	0·975–1·125	1·05	0·106	(10·10)
P_4	12	1·350–1·525	1·44	0·048	3·33	10	1·050–1·250	1·18	0·070	5·89
$M_{1/2}$	88	1·425–1·700	1·57	0·066	4·18	96	1·250–1·500	1·35	0·056	4·17
M_3	42	1·550–1·850	1·70	0·082	4·83	40	1·150–1·500	1·34	0·063	4·72

The specimens figured in Plate 18 show some of the range of variation in $M^{1/2}$s relevant to an understanding of the character developments detailed in Table 20. Metalophule I may be a complete ridge (fig. 8), a lingually restricted ridge (figs 3, 9), reduced to just metaconule 1 (fig. 2) or missing (fig. 7). Size 1 is shown in figs 2–3, size 2 in fig. 9 and size 3 in fig. 12. There may be a minor ridge of enamel joining metaconule 1 to either the endoloph, hypocone, metalophule II or a combination of the three. Fig. 9 shows links to both the endoloph and metalophule II. Metaconule 2 is sometimes present (figs 8, 11) but usually absent (figs 2–3, 7, 9–10, 12). Enamel wrinkling may be fine low beading (fig. 2) or finely (fig. 7) to coarsely (fig. 9) reticulate, and may show degrees of obscuration by wear (figs 8, 12). The sinus may be shallow (fig. 9), of medium depth (fig. 2) or deep (fig. 12); it is nearly always complete. The mesostyle has been given five arbitrary size numbers: 0 (fig. 10), 1 (fig. 8), 2 (fig. 2), 3 (figs 11–12), 4 (figs 3, 7, 9). Its buccal saliency is sometimes but not always related to its size; e.g. there may be an ectoflexus (fig. 10) or the mesostyle may be non-salient (grade 1: fig. 8) or salient in two size grades (2: fig. 3; 3: fig. 9). The mesostyle may be a circular object (fig. 2) or it may be elongated into a partial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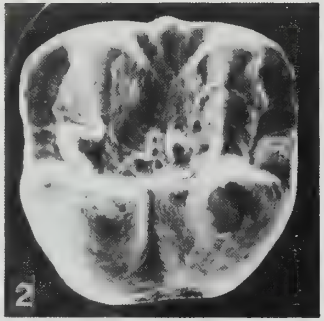
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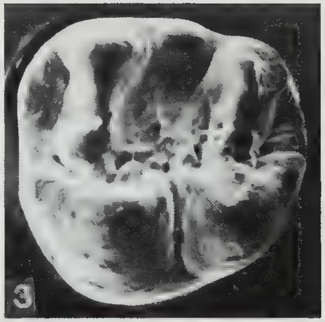
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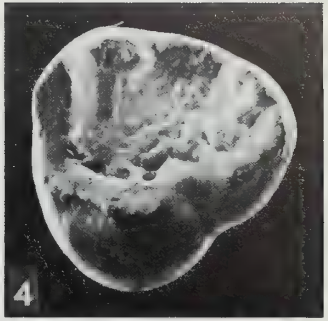
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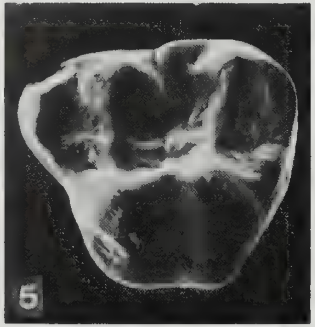
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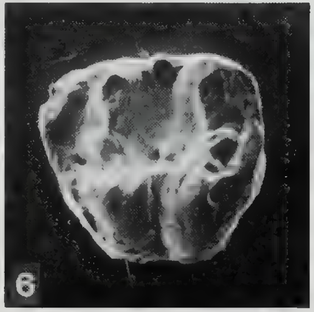
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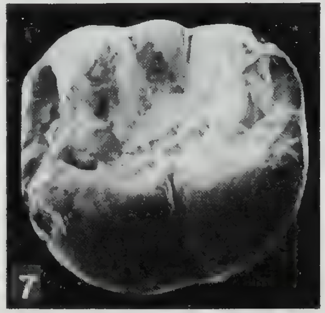
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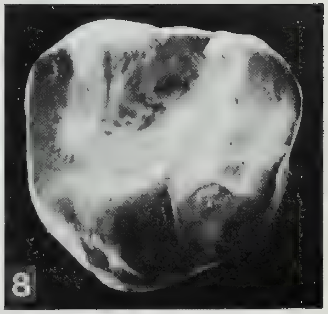
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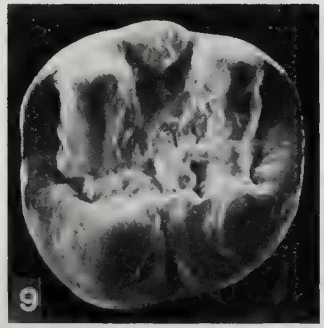
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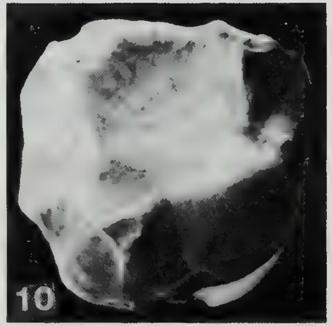
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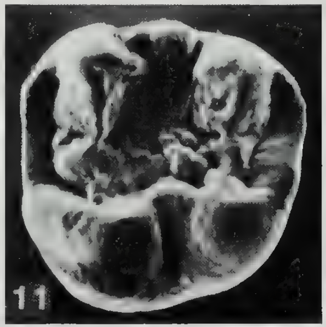
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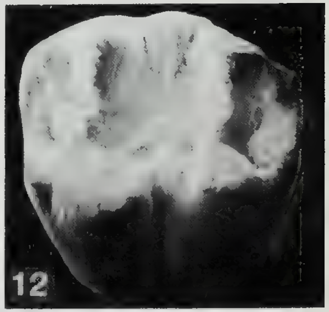
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Table 20 Percentage character analysis of upper cheek teeth of *Suevosciurus authodon* from Creechbarrow. For explanation see Table 14.

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Metalophule I shape: metaconule 1 only (1), ridge (2) (10) (0) (18) (30) (0)	1	70		88·9	83·3	
	2	30		11·1	16·7	
Metalophule I size (13) (15) (19) (31) (0)	0	23·1	100	5·3	3·2	
	1	23·1	0	31·6	19·4	
	2	46·1	0	42·1	54·8	
	3	7·7	0	21·0	22·6	
Metalophule I joins endoloph (1), hypocone (2), metalophule II (3), endoloph and hypocone (4), hypocone and metalophule II (5), endoloph and metalophule II (6), all three (7), none (0) (10) (0) (18) (30) (0)	0	10		39·0	13·3	
	1	0		50·0	40·0	
	2	60		5·5	13·3	
	3	30		0	16·8	
	4	0		5·5	0	
	5	0		0	3·3	
	6	0		0	10·0	
	7	0		0	3·3	
Metalophule II broken/unbroken (20) (20) (23) (55) (12)	B	5	25	0	12·7	83·3
	U	95	75	100	87·3	16·7
Enamel wrinkling (0–3) (5) (16) (10) (22) (11)	0	100	0	10	0	0
	1	0	0	60	63·6	0
	2	0	50	30	36·4	45·5
	3	0	50	0	0	54·5
Mesostyle size (0–4) (18) (21) (22) (52) (16)	0	0	0	0	1·9	12·5
	1	11·1	0	9·1	1·9	0
	2	44·4	4·8	9·1	32·8	0
	3	38·9	47·6	59·1	36·5	25·0
	4	5·6	47·6	22·7	26·9	62·5
Mesostyle saliency: prominent (3), slight (2), non (1), ectoflexus (0) (19) (20) (21) (51) (20)	0	26·3	30	4·8	2·0	0
	1	68·4	60	57·1	43·1	40
	2	5·3	10	33·3	35·3	45
	3	0	0	4·8	19·6	15
Mesostyle mesiodistally elongated (19) (21) (22) (52) (21)	0	100	66·7	100	86·5	0
	1	0	33·3	0	13·5	100
Mesoloph length (0–2) (18) (21) (22) (52) (21)	0	5·6	66·7	27·3	44·2	85·7
	1	61·1	23·8	54·5	46·2	14·3
	2	33·3	9·5	18·2	9·6	0

Table 20 (*continued*)

Plate 18 Scanning electron micrographs of upper cheek teeth of *Suevosciurus authodon* sp. nov. from Creechbarrow, × 25. Fig. 1, right P^4 (reversed) (M35795). Fig. 2, left M$^{1/2}$ (M^1?) (M35821). Fig. 3, left M$^{1/2}$ (M^2?) (M35481). Fig. 4, right M^3 (reversed) (M35489). Fig. 5, **holotype** right DP^4 (reversed) (M35469). Fig. 6, left DP^4 (M36447). Fig. 7, right M$^{1/2}$ (M^2?) (reversed) (M35861). Fig. 8, right M$^{1/2}$ (M^2?) (reversed) (M35855). Fig. 9, left M$^{1/2}$ (M^2?) (M35833). Fig. 10, left M$^{1/2}$ (M^2?) (M35838). Fig. 11, right M$^{1/2}$ (reversed) (M35860). Fig. 12, left M$^{1/2}$ (M^2?) (M35844). See p. 315.

Table 20 continued

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Protolophule I broken/unbroken	B	9·5	50	4·4	3·6	23·5
(21) (16) (23) (55) (17)	U	90·5	50	95·6	96·4	76·5
Metaconule 2 absence/presence	0	66·7	65	78·3	62·3	
(21) (20) (23) (53) (0)	1	33·3	35	21·7	37·7	
Hypolophule absent (0), partial	0	85·7	79·0	95·2	70·4	
(1), complete (2)	1	14·3	10·5	4·8	3·7	
(21) (19) (21) (54) (0)	2	0	10·5	0	25·9	
Posteroloph broken/unbroken lingually	B	33·3	36·8	13·0	1·8	
(21) (19) (23) (55) (0)	U	66·7	63·2	87·0	98·2	
Mesocone absence/presence	0	100	100	94·1	91·9	100
(21) (18) (18) (40) (14)	1	0	0	5·9	8·1	0
Sinus depth: shallow (1) to	1	0	0	0	0	4·8
deep (4)	2	5·3	20	4·4	18·2	14·3
(19) (20) (23) (55) (21)	3	68·4	75	52·2	65·5	57·1
	4	26·3	5	43·4	16·3	23·8
Protostyle absence/presence	0	52·9	100	26·3	59·5	75
(17) (18) (19) (37) (16)	1	47·1	0	73·7	40·5	25
Hypostyle absence/presence	0	80·9	73·7	33·3	47·2	
(21) (19) (18) (36) (0)	1	19·1	26·3	66·7	52·8	
Paraconule absent (0), small (1),	0	0	5	0	0	0
large (2)	1	0	5	4·4	5·5	36·8
(21) (20) (23) (55) (19)	2	100	90	95·6	94·5	63·2
Endoloph broken (1), complete (2)	1	0	21·1	4·4	3·6	0
(20) (19) (23) (55) (15)	2	100	78·9	95·6	96·4	100
DP^4 parastyle bicuspid	0	53·3				
(15)	1	46·7				
DP^4 mesiolingual margin concave	0	60				
(20)	1	40				

mesoloph (grade 1: fig. 7; or 2: fig. 12); alternatively it may be mesiodistally elongated (figs 3, 9). Whereas in advanced species of *Suevosciurus* the $M^{1\ 2}$ paraconule is often reduced, this is so in only four Creechbarrow specimens (e.g. fig. 9). Metalophule II may be broken buccal and/or lingual to the position of metaconule 2 (whether present or absent) and there may be a hypolophule (fig. 7). Other minor cusps which may be present are protostyle (= anterocone), mesocone and hypostyle (fig. 12).

When the usual method of distinguishing M^1 from M^2 (see under Taxonomic Treatment of the Pseudosciuridae, p. 298) was used for this species, it was found that M^2s outnumbered M^1s two to one. One explanation is that the M^2 type morphology commonly occurred in M^1.

On M^3, although the paraconule is often weaker than on M^{1-2}, it may also be accompanied by a crest which joins it to the anteroloph, as on one M^3 of *Sciuroides rissonei* (M36115). Because of the distal tapering of the outline of this tooth, a metacone is present, as shown in Pl. 18, fig. 4, in only three out of twenty specimens.

The $M_{1/2}$s are less variable than the upper molars. The ectolophid/hypolophulid connection varies from at or very close to the hypoconid (Pl. 17, fig. 8) to about a quarter the distance along the hypolophulid from the hypoconid (fig. 9). The anteroconid is always present and often large; fig. 8 shows a size 1 anteroconid, fig. 9 a size 2 and fig. 12 a size 4. Figs 8–9 show the typical 60–70% filling of the sinusid by the mesoconid. Enamel wrinkling resembles that on M^{1-2}. Most *Suevosciurus* sp. from the Mammal Bed of Hordle Cliff have the buccal end of the mesoconid fused to the hypoconid. Schmidt-Kittler (1971*a*: 44) noted this occasionally also in *S. fraasi* from southern Germany. Proportionately fewer specimens from Creechbarrow than from Hordle have this character.

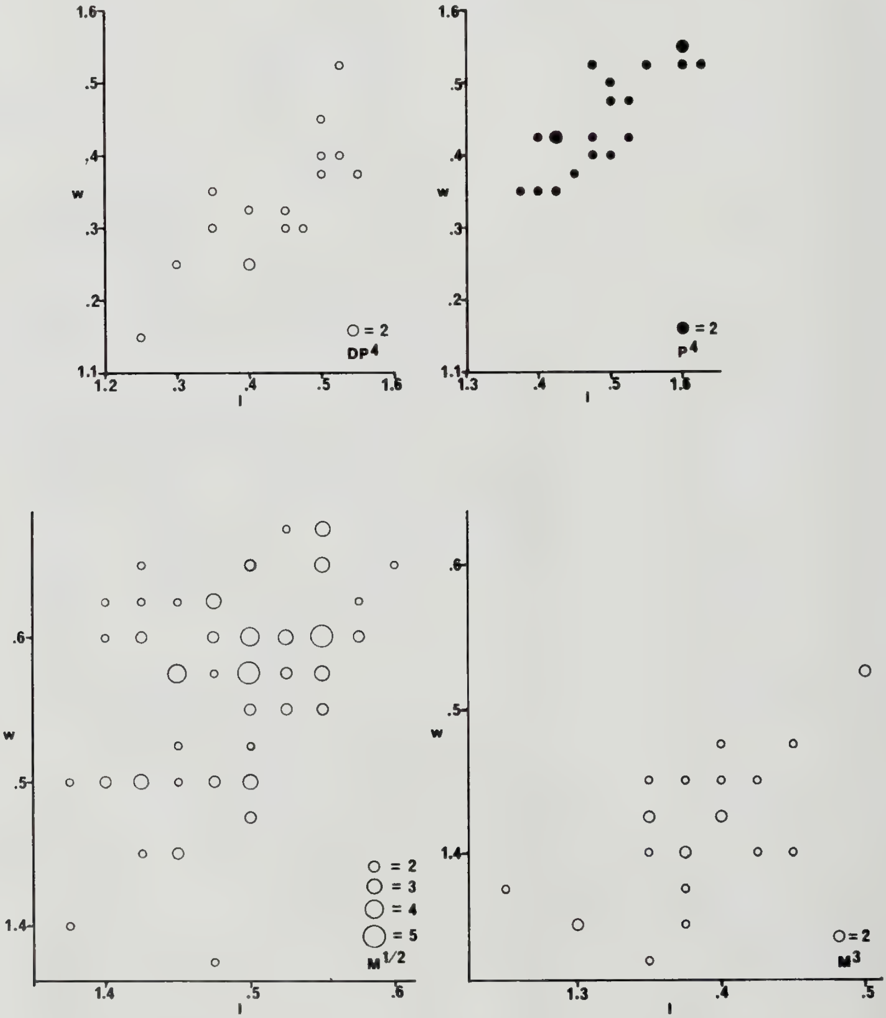
PHYLOGENETIC RELATIONSHIPS WITH OTHER SPECIES OF *Suevosciurus*. *S. authodon* appears primitive in its retention of P^4_4; relatively short DP^4; normally large paraconule; normal presence of

Table 21 Percentage character analysis of lower cheek teeth of *Suevosciurus authodon* from Creechbarrow. For explanation see Table 14.

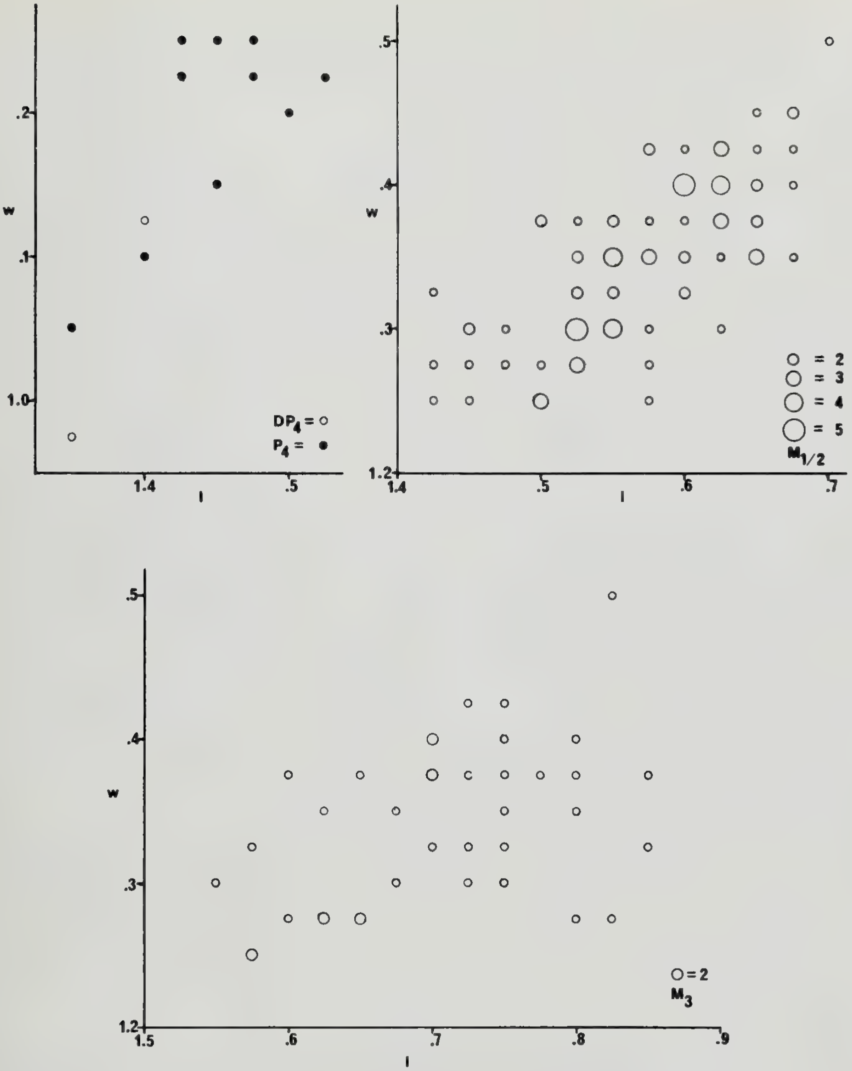
Characters + (N) of respective teeth	Scoring units	DP_4	P_4	M_1	M_2	M_3
Distance along hypolophulid from hypoconid of junction with ectolophid (2) (9) (32) (34) (32)	$<\frac{1}{4}$	50	55·6	78	47	65·6
	$\frac{1}{4}$	50	44·4	22	53	31·3
	no link	0	0	0	0	3·1
Anteroconid size (1–4) (0) (0) (32) (35) (35)	1			3·1	22·9	74·3
	2			21·9	31·4	25·7
	3			59·4	37·1	0
	4			15·6	8·6	0
Anterolophulid absent (0), weak (1) (0) (0) (31) (30) (27)	0			80·7	86·7	40·7
	1			19·3	13·3	59·3
Mesoconid length as % depth of sinusid (2) (9) (31) (36) (33)	50	0	11·1	22·6	27·8	6·1
	60	50	22·2	35·5	19·4	12·1
	70	0	33·4	35·5	27·8	33·3
	80	50	22·2	6·4	13·9	27·3
	90	0	11·1	0	2·8	15·1
	100	0	0	0	8·3	6·1
Mesoconid fused buccally with hypoconid (2) (9) (31) (36) (33)	0	100	100	67·7	78·8	78·8
	1	0	0	32·3	21·2	21·2
Enamel wrinkling (0–3) (2) (6) (23) (18) (21)	0	100	0	8·7	22·2	0
	1	0	0	73·9	50·0	14·2
	2	0	50	17·4	27·8	42·9
	3	0	50	0	0	42·9
Mesostylid absence/presence (2) (9) (33) (38) (26)	0	100	100	93·9	100	70
	1	0	0	6·1	0	30
Ectostylid absence/presence (2) (9) (32) (37) (33)	0	100	100	96·9	83·8	100
	1	0	0	3·1	16·2	0
Hypoconulid absence/presence (2) (9) (33) (32) (30)	0	100	44·4	51·5	71·9	86·7
	1	0	55·6	48·5	28·1	13·3
Distal crest to hypolophulid absence/presence (2) (9) (34) (35) (26)	0	100	77·8	97·1	85·7	96·1
	1	0	22·2	2·9	14·3	3·9

incomplete metalophule I with large metaconule 1; and normally complete M_3 hypolophulid. In all other assemblages of *Suevosciurus* species where cheek teeth mesial to the molars are known, only DP$\frac{4}{4}$ (never P$\frac{4}{4}$) have been found; this tooth tends to have a higher length/width ratio than in *S. authodon* (except in the holotype of *S. ehingensis*), although there is some overlap. In assemblages from the early Ludian of the Isle of Wight a short incomplete metalophule I is occasionally present (Bosma 1974: 40); it also occurs in the Bavarian assemblages (Schmidt-Kittler 1971*a*: text-fig. 17). In assemblages of *Suevosciurus* other than from Creechbarrow, the $M^{1/2}$ metaconule 2 is normally missing. It is not mentioned by Bosma (1974) as occurring in the Isle of Wight assemblages and only occasionally as a vestigial feature by Schmidt-Kittler (1971*a*: 40, text-fig. 17a).

Attempts to compare the Creechbarrow *Suevosciurus* with existing material from the literature are hampered by the lack of numerically delineated information on morphological variation and the belief that the various species only differ in size.



Text-figure 36 Scatter diagrams of length (l) against width (w) in DP^4, P^4, $M^{1/2}$ and M^3 of *Suevosciurus authodon* sp. nov. from Creechbarrow. Measurements in millimetres.

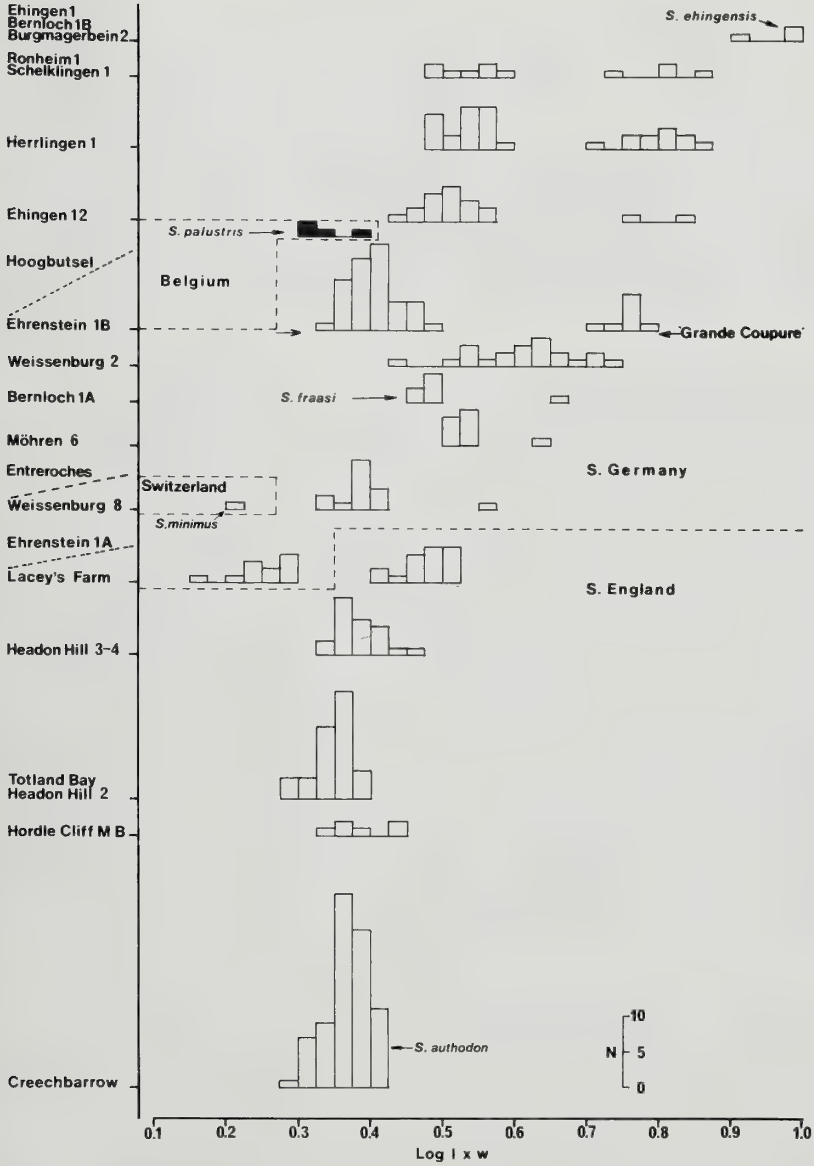


Text-figure 37 Scatter diagrams of length (l) against width (w) in DP_4, P_4, $M_{1/2}$ and M_3 of *Suevosciurus authodon* sp. nov. from Creechbarrow. Measurements in millimetres.

Schmidt-Kittler (1971*a*) identified two principal lineages of *Suevosciurus* which differed in size where found together at any one locality. The sequence of fissure-fill localities he dated by correlating other elements of their mammal faunas with those known from stratified sequences elsewhere in Europe. The smaller lineage he referred to *S. fraasi*, the larger to *S. ehingensis*. Each lineage fluctuated in size somewhat but there was a net size increase with time. Some very small teeth from Ehrenstein 1A and Weissenburg 6 he removed from his two lineages and identified as *S. minimus* on the basis of size. Bosma (1974) also demonstrated a slight size increase in a sequence of three superposed horizons in the Isle of Wight Ludian. She noted the problem of identification posed by those of Schmidt-Kittler's assemblages with only one species of *Suevosciurus*, as there is overlap if all assemblages are considered together. To avoid identifying them by horizon determined in turn by the associated fauna, she suggested a classification based on arbitrary size groupings. The result was the identification of parts of the *S. ehingensis* lineage as *S. fraasi* and parts of the *S. fraasi* lineage as *S. palustris*. In addition, she calculated that there was an undescribed species intermediate in size between *S. fraasi* and *S. ehingensis*. On the same basis, material from the Headon Beds was identified as *S. palustris* and that from the Osborne Beds (Bosma & Insole 1976) as *S. fraasi*.

Two different displays of the published data plus some new data are presented here in an attempt to test the credibility of the lineages and also to search for ways of identifying species other than by purely single parameters or by stratigraphy. Firstly (Text-fig. 38) histograms of the log of length × width of $M^{1/2}$ have been plotted in stratigraphical order. The record is not as dense as it is for part of the Wyoming early Eocene (see Gingerich 1976*a*) and more than one phylogenetic interpretation is possible. After the Grande Coupure most of the Bavarian localities contain a larger and a smaller species which show only a slight size increase with time. Of these the smaller one can readily be identified with *S. fraasi* on size. The larger, however, is considerably smaller than the type assemblage of *S. ehingensis* from the later (Antoingt Zone) Ehingen 1 locality. Where two species are present in Bavarian fissure fillings prior to the Grande Coupure, there is more size variation between localities and consequent overlap in total. Moreover, the smaller species is in most cases the more abundant, except in the last locality prior to the Grande Coupure (Weissenburg 2) where the larger has a wide observed range into which the one smaller specimen (doubtfully attributed by Schmidt-Kittler to *S. fraasi*) could possibly be incorporated. If the two post-Grand Coupure lineages could be shown to be derived from this single variable species, then the smaller one could no longer be identified as *S. fraasi*, whose type locality is slightly older. On the other hand, the Weissenburg 2 histogram is bimodal and the length measurements produce a coefficient of variation of 9·11, twice that of the unimodal assemblages with at least twenty specimens. It appears thus that two species are represented in the Weissenburg 2 assemblage, but more than just the smallest specimen should be referred to *S. fraasi* (see Schmidt-Kittler 1971*a*: 109). Overlap of measurements, however, means that it is impossible to identify all specimens. If more specimens from earlier pre-Grande Coupure Bavarian sites were known, they would probably overlap like those of Weissenburg 2. Nevertheless, the presence of the same two lineages from Weissenburg 8 until Ronheim 1 is supported by the length × width histograms.

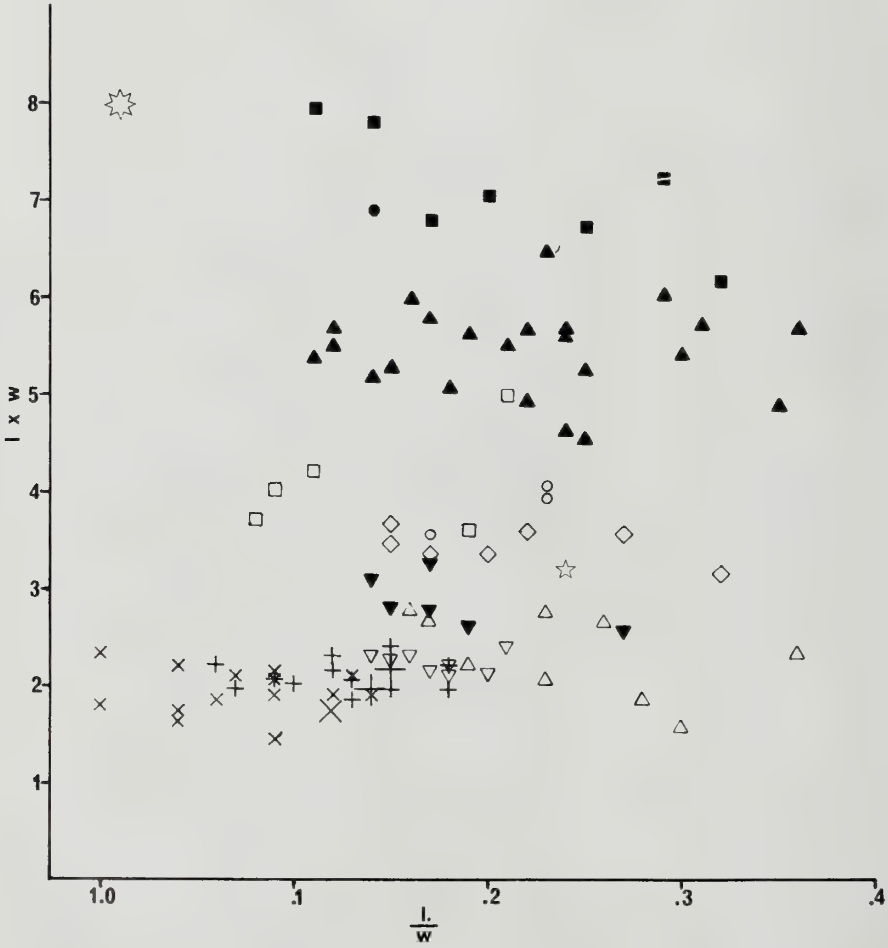
Turning now to the Isle of Wight assemblages, those from the Headon Beds were identified by Bosma (1974) as *S. palustris*. She nevertheless noted that on the single upper molar of this species in the GIU from the type locality, the mesostyle was hardly developed. The holotype and three topotype $M^{1/2}$s in the IRSNB, now cleaned of wax, show a similar poor development of the mesostyle; so does GIU HB801. Schmidt-Kittler (1971*a*: 40) mentioned the presence of well-developed mesostyles in his assemblages and Bosma (1974: 40) noted that although variable the mesostyle was usually relatively high in her assemblages. Out of 74 $M^{1/2}$s from Creechbarrow, only 3 have mesostyles as poorly developed as those of *S. palustris*. Specimens from the Osborne Beds of Lacey's Farm Quarry, Isle of Wight, were identified by Bosma & Insole (1976) as *S. fraasi* on the basis of size. They are intermediate between the larger and smaller species present at Weissenburg 8, a locality probably only slightly younger than Lacey's Farm Quarry. They overlap with the smaller species and probably would also overlap with the larger species if more specimens were known. The Lacey's Farm Quarry assemblage appears a good candidate for potential common ancestry of both the larger and smaller lineages. Alternatively, *S. minimus* from Ehrenstein 1A could have given rise to the smaller species and the Lacey's Farm Quarry assemblage to the larger species. Unfortunately little is known of *S. minimus* from any locality so that assessment of its position in the phylogeny is not yet possible. Either of the two above alternatives appear more plausible in the light of the Isle of Wight material, however, than Schmidt-Kittler's (1971*a*: 119) idea that *S. minimus* was the common ancestor of both lineages. The placing of *S. minimus* in an ancestral position probably arose because he thought the holotype came from the Bartonian fissure of Eclépens-Gare. However, a label with the specimen in the LGM in Stehlin's writing gives 'Entreroches', which is a later Ludian fissure. That this is the correct provenance is supported by the record of 'une très petite mandibule inférieure portant quatre molaires et une incisive' belonging to a 'Rongeur' by Harpe & Gaudin (1854: 127).



Text-figure 38 Histograms of log. length × width in stratigraphic order of $M^{1/2}$ of species of *Suevosciurus* from localities in England, Switzerland, southern Germany and Belgium, spanning Bartonian to Stampian. For measurements and references to localities see Cray (1973), Bosma (1974), Bosma & Insole (1976), Insole (1972) and herein for England, Stehlin (1903) for Switzerland, Schmidt-Kittler (1971*a*) for southern Germany and Misonne (1957) for Belgium. The histogram of *S. palustris* (Misonne) is shown solid to indicate that it is morphologically separable from its contemporary *S. fraasi* Major from Ehrenstein 1B. The single plot of *S. minimus* (Major) from Entreroches is estimated from the unique M_1, by squaring its length. Names of species arrowed indicate type assemblages or age of type assemblage (*S. fraasi*).

The second combination of parameters is shown in Text-fig. 39. It plots length × width against length/width of DP^4. The lowest length/width ratio is shared by the Creechbarrow species and the holotype of *S. ehingensis*, which can be distinguished easily on absolute size. The larger species from Ehrenstein 1B, Herrlingen 1 and Schelklingen 1 have higher ratios. The smaller species from Bernloch 1A, Ehrenstein 1B, Ehingen 12, Herrlingen 1, Schelklingen 1 and Ronheim 1 in total spans the ratio of the larger species but is less variable (possibly an artifact of lower numbers) in each locality; in the smaller species the assemblages with the smaller teeth have a higher length/width ratio than those with the larger teeth.

Specimens from Lacey's Farm Quarry fit easily within the range of *S. fraasi*. However, as no pre-Grande Coupure DP^4s belonging to the larger Bavarian species are known, no concomitant contrast can be made. The teeth from the Headon Beds are similar in size to the smallest in the smaller Bavarian lineage from Ehrenstein 1B. Both were identified by Bosma as *S. palustris*.



Text-figure 39 Scatter diagram of length × width against length/width in DP^4 of species of *Suevosciurus*. Key: × = Creechbarrow; + = HH2 and TB; ▽ = HH3–4; ▼ = Lacey's Farm Quarry; ☆ = *S. fraasi* Major from Bernloch 1A; △ = *S. fraasi* from Ehrenstein 1B; ▲ = the larger lineage from Ehrenstein 1B; ◇ = *S. fraasi* from Ehingen 12; ☐ = *S. fraasi* from Herrlingen 1; ■ = the larger lineage from Herrlingen 1; ○ = *S. fraasi* from Ronheim 1 and Schelklingen 1; ● = the larger lineage from Schelklingen 1; and ☆ = *S. ehingensis* Dehm from Ehingen 1. For data sources see Text-fig. 38, p. 325.

The Headon Beds teeth can be distinguished by their length/width ratios, which are intermediate between those from Ehrenstein 1B and those from Creechbarrow, slightly overlapping both. Their stratigraphical trend is towards higher length/width ratio. In the light of the few Hordle Cliff specimens and the histograms shown here, Bosma's (1974) claimed size increase through the Headon Beds does not appear to be a significant trend. On the basis of mesostyle size, neither the Headon Beds *Suevosciurus* nor the smallest members of the smaller Bavarian lineage deserves to be identified as *S. palustris.*

Can *Suevosciurus authodon* be considered the common ancestor for all later species of the genus? It *is* the oldest and most primitive known. No assemblages with two species are known until Ehrenstein 1A. Without a better Bartonian record, it is not possible to judge whether or not *S. authodon* was actually the common ancestral species for *Suevosciurus*, but it nevertheless represents a good morphological ancestor. The absence of any authenticated records of *Suevosciurus* from non-British Bartonian sites suggests that it may have originated in the area of southern England and later spread to the rest of Europe.

RELATIONSHIP WITH *Treposciurus.* Although *Suevosciurus authodon* has many of the characters of later *Suevosciurus* species, these are often less developed or occur in a smaller percentage of individuals in the assemblage. Moreover, its ability to replace $DP\frac{4}{4}$ with $P\frac{4}{4}$ and the characters of this latter tooth closely resemble *Treposciurus helveticus preecei.* Close relationship is indicated and it is likely that they had a very recent common ancestry within the Bartonian.

RECOMMENDATIONS ON APPLICATION OF CURRENT SPECIFIC NAMES. 1. *S. ehingensis* should be restricted to material from Ehingen 1, Bernloch 1B and Burgmagerbein 2, comprising very large teeth and a DP^4 with a length/width ratio of about 1.

2. *S. palustris* should be restricted to the small teeth from Hoogbutsel with upper molar mesostyles minute or missing.

3. *S. fraasi* should be used for the smaller of the two main Bavarian lineages, characterized by having DP^4 with a very prominent parastyle.

4. *S. minimus* should be used for the holotype M_{1-3} from Entreroches, about which more information is needed before its status can be assessed, and the isolated molars from Ehrenstein 1A and Weissenburg 6.

This leaves, as two definable unnamed species, members of the main larger Bavarian lineage (referred by Schmidt-Kittler 1971*a* to *S. ehingensis*) and the small teeth from the Headon Beds (referred by Bosma 1974 to *S. palustris*). More problematical are the teeth from Lacey's Farm Quarry. More material from critical levels and in more geographical areas would improve our knowledge of the interrelationships within this complex genus, whose biostratigraphical potential is high.

Order **APATOTHERIA** Scott & Jepsen 1936

I follow Sigé (1975) and Russell *et al.* (1979) in recognizing this group as a distinct order. Its position herein adjacent to the Carnivora and distant from the Proteutheria reflects its relationships with the palaeoryctids as advocated by Szalay (1968), themselves showing specializations towards creodonts, carnivores and condylarths (see Van Valen, 1966). It comprises only one family unless *Aethomylos* Novacek 1976 is an apatothere (see Novacek, 1976: 40–44, figs 16–19).

Family **APATEMYIDAE** Matthew 1909

TYPE GENUS. *Apatemys* Marsh 1872.

INCLUDED GENERA. *Jepsenella* Simpson 1940; *Labidolemur* Matthew & Granger 1921; *Stehlinella* Matthew 1929*c*; *Sinclairella* Jepsen 1934; *Eochiromys* Teilhard 1927; *Heterohyus* Gervais 1852.

RANGE. Middle Palaeocene–Oligocene, North America; late Palaeocene–late Eocene, Europe.

DIAGNOSIS. See McKenna (1963: 13).

Table 22 Distribution of characters (except size) in the different post-Ypresian species of *Heterohyus*. As *H. heufelderi* and *H. gracilis* appear identical in all characters except the relative sizes of P_3 and P_4 based on alveoli, characters virtually unknown for the other species, they are considered together. Characters are estimated as primitive (−) or advanced (+) based on outgroup comparison with the rest of the Apatemyidae. Characters 1 to 12 involve upper molars; charactes 13 to 25 involve lower molars. Lack of information on a character is indicated by '?'.

	Character	State		*H. armatus*	*H. europaeus*	*H. gracilis* and *H. heufelderi*	*H. sudrei*	*H.* sp., Malpérié	*H. nanus*	*H. morinionensis*	*H. quercyi*
		primitive	advanced								
1	M^1 parastyle strength	weak	strong	?	−	?	+	?	+	?	+
2	M^2 buccally salient parastyle	yes	no	?	?	−	?	+	−	+	+
3	M^2 ditto strength	strong	weak	?	?	+	?		−		
4	M^2 parastyle mesially salient	yes	no	?	?	+	?	+	+	−	−
5	M^2 ectoflexus	shallow	deep	?	?	+	+	−	+	−	−
6	M^{1-2} postmetacrista	present	absent	?	+	−	−	−	−	−	−
7	M^{1-2} postmetacrista strength	weak	strong	?		−	+	−	−	−	−
8	M hypocone	small	large	?	−	−	−	−	−	+	+
9	M postprotocingulum joining hypocone	no	yes	?	−	−	+	−	−	−	−
10	M postprotocrista	yes	no	?	+	−	+	+	+	−	−
11	M postprotocrista strength	weak	strong	?		−				−	+
12	M posthypocrista	weak	strong	?	−	+	+	+	−	−	−
13	M_2 lingual hypoconulid	no	yes	−	+	−	−	?	−	−	?
14	M_{1-2} entoconid notch	no	yes	−	−	+	+	?	−	−	?
15	M talonid length	short	long	−	−	+	+	?	−	−	−
16	M trigonid length	long	short	−	+	−	−	?	+	+	+
17	M entoconid	weak	strong	+	+	−	−	?	+	+	+ ?
18	M paraconid	weak	strong	+ ?	+	−	+	?	−	−	+
19	M mesial paracristid limb	absent	present	+	+	−	−	?	−	−	+
20	M ditto strength	weak	strong	+	−			?			+
21	M postcristid	transverse	oblique	+	−	+	+	?	−	−	−
22	$M_3 : M_2$ length ratio	low	high	−/+	−	−	?	?	+	−	+
23	M_3 hypoconulid cusp length	short	long	−	−	−	?	?	−	−	+
24	M_3 hypoconulid lobe extending talonid	no	yes	−/+	−	−	?	?	+	−	−
25	M_3 hypoconulid bulging buccally	no	yes	−/+	−	−	?	?	−	+	−
26	Lower incisor	narrow	wide	−	+	−	?	?	−	?	−
27	Depth of mandible	shallow	deep	−	+	−	?	?	−	?	−
28	Ascending ramus	behind M_3	beside M_3	−	+	−	?	?	−	?	−

Genus ***HETEROHYUS*** Gervais 1852

[incl. *Necrosorex* Filhol 1890*c*, *Amphichiromys* and *Heterochiromys* Stehlin 1916, *Heterohyus* (*Chardinyus*) and *H.* (*Gardonyus*) Sigé 1975]

TYPE SPECIES. *H. armatus* Gervais 1852. Middle Lutetian, Bouxwiller, France.

INCLUDED SPECIES. *H. europaeus* (Stehlin 1916) Teilhard 1922; *H. gracilis* (Stehlin 1916) Teilhard 1922; *H. heufelderi* Heller 1930 (doubtfully distinct from *H. gracilis*, but see discussion in Russell *et al.*, 1979: 226); *H. sudrei* Sigé 1975; *H. quercyi* (Filhol 1890*c*) Teilhard 1922; *H. nanus* Teilhard 1922; *H. morinionensis* sp. nov.; *H.* sp. from Malpérié and La Bouffie (see Sigé 1975: 665); *H.* sp. from Hordle Cliff (see Cray 1973: 63–64); *H.* sp. from Mutigny; *H.* spp. 1, 2, 3 from Avenay; *H.* spp. [1, 2] from Grauves and Cuis (see Russell *et al.*, 1979: 227–231).

RANGE. Ypresian–Ludian, France; late Lutetian, Switzerland; early Lutetian, D.D.R.; Marinesian–early Ludian, England.

DIAGNOSIS. See Sigé (1975: 656) for the most recent formal diagnosis; but see Russell *et al.* (1979: 222–226) for comprehensive discussion of generic characters.

DISCUSSION. Species of this genus, like the others in the Apatemyidae, are rare faunal elements and are known mainly from scattered, isolated teeth. A few jaws are known but the only specimen with upper and lower teeth associated (referred specimen of *H. quercyi*) is lost (*fide* Sigé 1975: 658). There are thus often problems in associating both different tooth types in a single row and uppers and lowers of the same species. Occlusal studies have not been published.

Table 22 shows the distribution of characters in the different post-Ypresian species (named and unnamed). Various attempts have been made in the past to divide the genus *Heterohyus* into different genera or subgenera (see synonymy list above, Sigé 1975 and Russell *et al.* 1979). The table shows that most of the available characters have a rather random distribution with few congruencies. The position is further complicated by the incompleteness of different taxa and the consequent poor overlap of parts known.

Small numbers of specimens restrict the knowledge of intraspecific variation. However, some such variation can be seen in Table 22 in characters 22, 24, and 25.

Neither a phenetic comparison, using all the characters, nor a cladistic one using only advanced characters (giving shared character states as percentages of the shared characters in both cases) give reliable results (see Table 23). The only exceptions are the very high dissimi-

Table 23 Number of character states in common between the different species of *Heterohyus*. Numbers are percentages of the total characters shared. Above the oblique line only advanced character states are used; below it all the character states are used. Characters are from Table 22.

	H. armatus	*H. europaeus*	*H. gracilis* and *H. heufelderi*	*H. sudrei*	*H.* sp., Malpérié	*H. nanus*	*H. morinionensis*	*H. quercyi*
H. armatus		19	7	25	–	20	17	36
H. europaeus	56		0	14	20	14	12	20
H. gracilis and *H. heufelderi*	67	30		33	40	8	0	0
H. sudrei	50	21	73		29	20	0	14
H. sp., Malpérié	–	60	67	57		22	11	11
H. nanus	73	57	60	47	67		10	17
H. morinionensis	58	59	50	20	56	62		20
H. quercyi	79	50	39	21	56	57	70	

larities of *H. gracilis/heufelderi* from *H. europaeus* and *H. quercyi* and of *H. morinionensis* from *H. gracilis/heufelderi* and *H. sudrei*. The only high similarities are *H. quercyi* with *H. armatus* and the *H.* sp. from Malpérié with *H. gracilis/heufelderi*, both artificially increased by the reduced number of shared anatomical parts known: *H. armatus* is only known from lower teeth, *H.* sp. from Malpérié only from one M^2. A further complication is that the upper dentition attributed to *H. quercyi* may not belong to this species. Future collecting in Europe may well allow more characters to be added for different species, thus helping to clarify relationships.

Heterohyus cf. ***sudrei*** Sigé 1975

(Pl. 19, fig. 7; Text-fig. 40E; Tables 22, 23)

HOLOTYPE of *H. sudrei*. Left M^3 (UM RBN5170). Lower Calcaire de Fons (Marinesian), Robiac-Nord, France.

RANGE of *H. sudrei*. Marinesian to early Ludian, France.

DIAGNOSIS of *H. sudrei*. See Sigé (1975: 657).

MATERIAL. Left $M_{1/2}$ talonid fragment (M35707).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. This specimen cannot be included in the best represented species from Creechbarrow (*H. morinionensis*) as it is slightly smaller; it has an entoconid notch, a slightly lower entoconid, and the buccal hypoconid wall is more vertical, meeting the postcristid at an acute angle when viewed distally. This compares well with *H. sudrei* (see Text-fig. 40E–F). In *H. morinionensis* and *H. nanus* the angle is 90° or more (Text-fig. 40A–D).

The rather longitudinal orientation of the cristid obliqua and its apparent buccal position of attachment to the trigonid suggests that the tooth is more likely to be an M_1 than an M_2. It has a large distal interstitial facet. Wear on the crown is slight. Just lingual of the midpoint of the postcristid on the mesial side is the faint swelling of a hypoconulid. There is a well-marked valley between this and the entoconid. Because of lingual breakage no width measurement is possible. However, it is slightly smaller than the M_2s of *H. sudrei* figured by Sigé (1975: pl. 2, figs 1–2).

Heterohyus aff. ***nanus*** Teilhard 1922

(Pl. 19, fig. 6; Text-fig. 40C; Table 24)

v. *1980 Heterohyus* sp. 2; Hooker & Insole: 40.

HOLOTYPE of *H. nanus*. Left mandibular ramus with incisor, P_4, $M_{2\ 3}$ (MNHN Qu8732). Phosphorites, Mémerlein, France.

RANGE of *H. nanus*. Marinesian to Ludian, France.

DIAGNOSIS of *H. nanus*. See Sigé (1975: 659).

MATERIAL. Left M_2 (M35709).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. The tooth is unworn but broken distolingually so that the entoconid is now missing. The angle that the postcristid makes with the buccal hypoconid wall, however, is obtuse, suggesting that the entoconid was developed as in *H. nanus* (i.e. larger than in *H. sudrei*). There is a small paraconid and the trigonid is open mesially, the mesial limb of the paracristid being absent, its place being taken by a mesial cingulum. Both trigonid and talonid are relatively short and the whole tooth is thus not much longer than wide.

All these characters suggest strong affinities with *H. nanus*. It is, however, smaller (Table 24), being closer in size to M_2 of *H.* sp. from Malpérié and La Bouffie (Sigé 1975: 665; pl. 1, figs 14–15). There appears to be a slight size increase with time for M^1, M^2 and M_2 from the

Table 24 Length (l) and trigonid (w_1) and talonid (w_2) width measurements of teeth of *Heterohyus* from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1		w_2
H. morinionensis:					
M35702	M^1	–		2·65	
M35703	M^2	2·85		–	
M35400	M^3	2·35		(3·50)	
M35705	M_2	2·40	2·00		1·95
M35706	M_3	–	–		1·90
H. aff. *nanus*:					
M35709	M_2	1·70	1·50		–

Robiac assemblage to those of Malpérié and Perrière (Sigé 1975: text-fig. 3); the Creechbarrow tooth might represent an earlier stage in this trend, but this can only be corroborated by the finding of more teeth and tooth types.

Heterohyus morinionensis sp. nov.

(Pl. 19, figs 1–5; Text-fig. 40D; Tables 22–24)

v. *1977b* *Heterohyus* (*Chardinyus*) sp.; Hooker: 141.
v. *1980* *Heterohyus* sp. 1; Hooker & Insole: 40.

NAME. Morinio, a Roman station in the present borough of Wareham, near Creechbarrow.

HOLOTYPE. Left M^3, M35400. Pl. 19, fig. 3.

PARATYPES. Left M^1 (M35702); right M^2 (M35703); right M^3 (M37119); lingual fragment of left M^3 (M35704); right M_2 (M35705); left M_3 talonid fragment (M35706).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

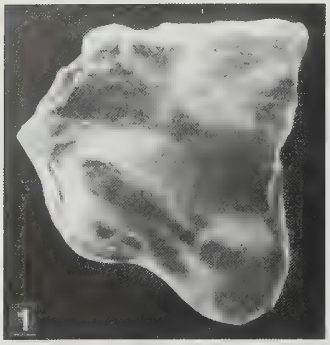
DIAGNOSIS. Medium–small species of *Heterohyus* (M^2 length 2·85 mm; see Table 24). M^2 with parastyle mesially but not buccally salient, and ectoflexus shallow. M^{1-2} with weak postmetacrista. Upper molars with large, well differentiated hypocone with weak posthypocrista and weak postprotocrista. M_2 without hypoconulid. M_{1-2} without entoconid notch. Lower molars with short trigonid and talonid; strong entoconid; weak paraconid; no mesial paracristid limb; and transverse postcristid. M_3/M_2 length ratio low. M_3 with short hypoconulid on short hypoconulid lobe, bulging buccally.

DESCRIPTION. M^1: The postprotocingulum is weak and the large, lingually salient hypocone is separated from it by a notch (Pl. 19, fig. 1). The parastyle and metastyle are broken away but the ectoflexus appears to have been at best very shallow. There is very weak postflexus. The distal cingulum peters out lingually but a continuation down the distal side of the hypocone takes the form of faint papillae.

M^2: This tooth is broken lingually and has a deep postflexus (Pl. 19, fig. 2). The metacone is formed lingually into a strong ridge confluent with the postprotocrista. There is a moderate ectoflexus.

M^3: On the holotype the parastyle is broken at its tip but when complete would have been very prominent buccally (Pl. 19, fig. 3). The postprotocrista appears very weak but may have been largely removed by wear. The two other fragmentary specimens show a constancy for the distinctness of the hypocone from the protocone, although the hypocone is slightly smaller in M35704 than in the other two specimens. M37119 is less worn than the holotype but shows the postprotocrista to be absent, a sharp even valley linking the trigon and talon basins.

M_2: The paraconid is broken away and the edge of the talonid notch, metaconid and entoconid slightly chipped (Pl. 19, fig. 4). Otherwise the tooth is well preserved, moderately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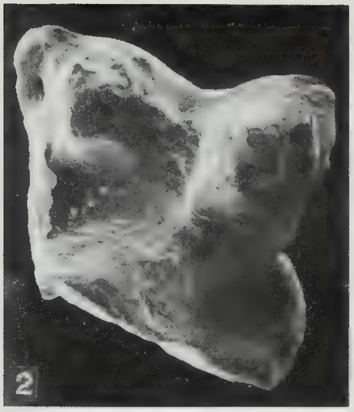
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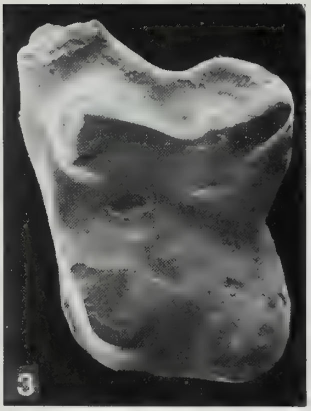
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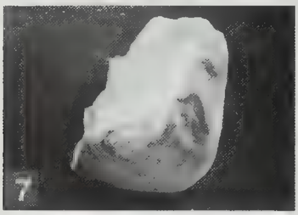
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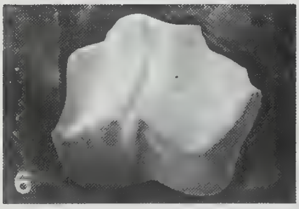
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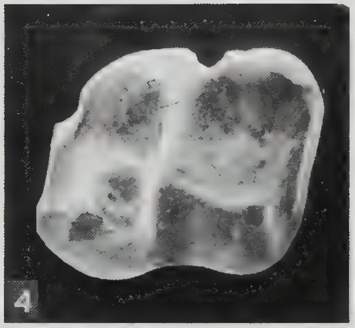
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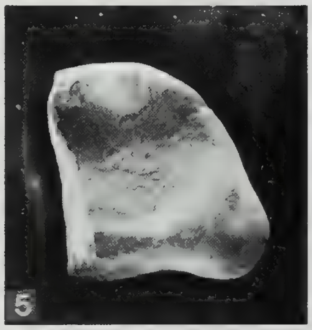
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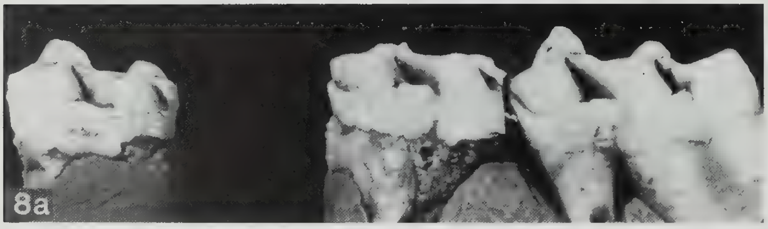
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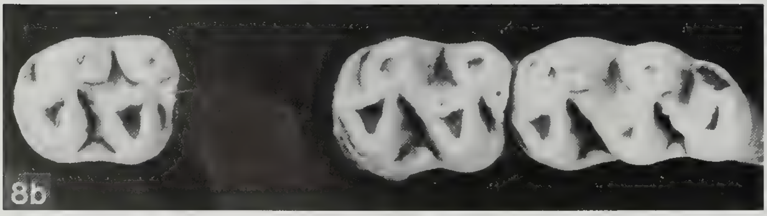
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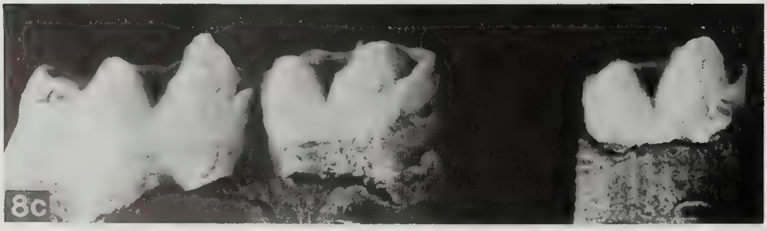
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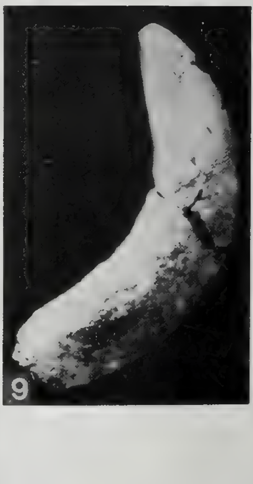
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worn with well-defined wear facets. The entoconid is distally positioned, confluent with the postcristid and there is no hypoconulid. A weak lingual rib on the protoconid half crosses the trigonid basin. There is a weak mesial cingulum but no mesial paracristid arm, so that the trigonid basin is open mesially.

M_3: This talonid fragment is truncated through the talonid notch and just behind the tip of the hypoconid (Pl. 19, fig. 5). Its most distinctive feature is the short buccal hypoconulid lobe. The hypoconulid appears to project buccally slightly beyond the hypoconid. The hypoconulid is like that in *H. quercyi* in one respect, that it is slightly constricted, unlike *H. nanus* where it merges imperceptibly in occlusal view with the rest of the talonid. Shape of the talonid appears to be variable (see discussion below).

DISCUSSION. When all characters are considered (including size), *H. morinionensis* is most similar to *H. quercyi*. This is, however, reliant on the correct attribution of the lost cranium and mandible figured by Teilhard (1922: text-fig. 39; pl. 4, figs 16–18). One must therefore first consider the likelihood of the specific association of this specimen with the holotype mandible with M_3.

In all the sufficiently known species of *Heterohyus* except *H. nanus* and *H. quercyi* there is a correlation between the upper molar postprotocrista and the lower molar paraconid. If the former is present the latter is weak; if the former is absent, the latter is strong. In *H. nanus*, lower molars with weak paraconids are 'associated' with upper molars without postprotocristae. In *H. quercyi*, M_3 with a strong paraconid is apparently associated with upper molars with postprotocristae.

Sigé (1975: pl. 1, figs 6–7) figured an M^1 and M^2 from Aubrelong 2 which he considered close in size and morphology to *H. quercyi*, but which he placed with some doubt in *H. sudrei*. His first identification as *H. quercyi*? is tentatively accepted here. These teeth are very similar to those of *H. morinionensis*, differing only in being slightly larger, having slightly stronger postprotocristae and shallower ectoflexus in M^2.

H. morinionensis upper molars occur at Creechbarrow with three different types of lower molars. Two of these have already been identified as *H.* cf. *sudrei* and *H.* aff. *nanus*, both being smaller than the third type, which are of appropriate size for the *H. morinionensis* upper molars. Furthermore, the M_2 of the third type (M35705) has a deeply grooved oblique buccal phase facet on the distal hypoconid wall (see Text-fig. 40D), which is considerably stronger and more oblique than the same facet on otherwise similar lower molars of *H. nanus*. It is most likely to have been caused by an M^2 metacone strengthened by the buccal end of a postprotocrista. Although the trigonid of M_3 is unknown in *H. morinionensis*, judged from a mandibular ramus of *H. nanus* (Sigé 1975: pl. 2, fig. 8a–c) the paraconid alters little in strength from M_1 to M_3. The M_3 paraconid in *H. morinionensis* is thus likely to have been considerably smaller than that of the holotype of *H. quercyi*.

The quality of Teilhard's (1922) retouched photographs of the referred cranium and mandible of *H. quercyi* is poor and the exact details of the teeth are confusing, the different scale photographs being partly contradictory. The lower teeth are mainly obscured, but M_1 (his pl. 4, fig. 17) does appear to have a strong paraconid, thus supporting his identification. It is possible

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Plate 19 Teeth of *Heterohyus* and *Lophiotherium* from Creechbarrow.

Figs 1–5 *Heterohyus morinionensis* sp. nov. Scanning electron micrographs of occlusal views of molars, × 16. Fig. 1, left M^1 (M35702). Fig. 2, right M^2 (reversed) (M35703). Fig. 3, **holotype** left M^3 (M35400). Fig. 4, right M_2 (reversed) (M35705). Fig. 5, left M_3 talonid fragment (M35706). See p. 331.

Fig. 6 *Heterohyus* aff. *nanus* Teilhard. Scanning electron micrograph of occlusal view of left M_2, × 16 (M35709). See p. 330.

Fig. 7 *Heterohyus* cf. *sudrei* Sigé. Scanning electron micrograph of occlusal view of left $M_{1\ 2}$ talonid fragment, × 16 (M35707). See p. 330.

Figs 8–9 *Lophiotherium siderolithicum* (Pictet). Light macrographs of lower teeth, × 3. Fig. 8a–c, associated left P_4, M_{2-3}; a, buccal, b, occlusal and c, lingual views (M37705). Fig. 9, lingual view of right lower canine (reversed) (M36828). See p. 347.

that the strengthening of the lower molar paraconid plus paracristid is a trend, independent of that occurring earlier in *H. armatus* and *H. europaeus*, and associated with similar strengthening of the upper molar postprotocrista and with a slight modification of the occlusal relationships of the upper and lower molars.

H. morinionensis also appears to differ from *H. quercyi* in having a buccally salient M^3 parastyle. The possibility cannot be excluded that this was broken in Teilhard's figured specimen. Two other characters, depth of M^2 ectoflexus and shape of the M_3 hypoconulid, may be intraspecifically variable. The first is supported by two M^2s of an undescribed species from Hordle Cliff, where the difference in depth is at least as great as between the Creechbarrow and Aubrelong 2 specimens. The second is supported by two specimens of *H. armatus* from Bouxwiller in the NMB (Bchs490 and Bchs306): the former is like the holotype (see Stehlin 1916: text-fig. 346b) where the hypoconulid is buccally situated and projecting and the lobe is short; the latter has a much longer median hypoconulid lobe.

Given the above conclusions, *H. morinionensis* is closely related to *H. quercyi* and is a good candidate both morphologically and stratigraphically to be its ancestor. *H. morinionensis* has no known specialized characters which would prevent such a possibility.

Heterohyus spp. indet.

(Text-fig. 40G–W)

MATERIAL. Six incisor fragments (M35699–700, M35708, M37116–8).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. These specimens show size differences, and some confusing morphological differences at least some of which are ontogenetic.

M35708 is much smaller than any of the others and almost certainly belongs to *H.* aff. *nanus* as represented by the M_2. It is rolled and the distal enamel band is little wider than the mesial one. The former was probably once wider, being worn away parallel to the buccal edge by post-mortem abrasion (Text-fig. 40U–W).

All the other incisor fragments are essentially the same size and presumably belong to the commoner *H. morinionensis* or to *H.* cf. *sudrei*, or both. The morphology of *Heterohyus* incisors has not been covered in much detail by authors and it is possible that they are not distinctive at species level. *H. sudrei* has no incisors attributed to it, whereas they are known for most of the other named species. The Creechbarrow incisors vary in width of the distal enamel band and cross-sectional shape.

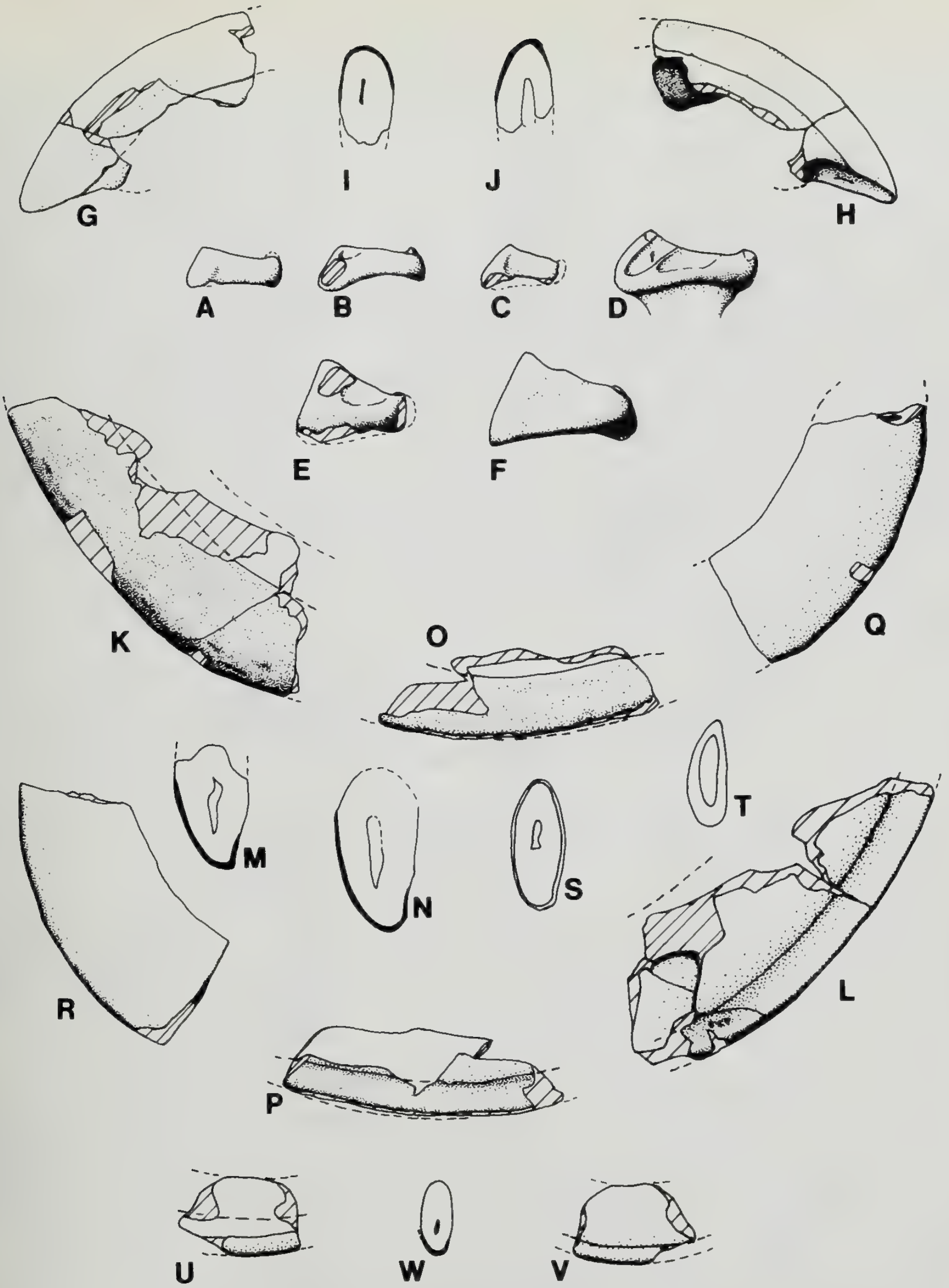
M35700 is the largest fragment. It is truncated at both ends but can be orientated by the apical narrowing of the pulp cavity. The enamel is slightly rugose, the distal enamel band is wide and the mesial enamel band concave. Apically there is a sharp mesiobuccal angle, but passing basally this angle becomes slightly rounded and begins to migrate lingually, thus making the buccal edge more evenly rounded and narrowing the mesial concavity. At this point, the mesial enamel has a noticeably pitted surface (Text-fig. 40K–N).

M35699 is a small fragment which appears to correspond in position to the apical end of M35700.

In M37117, the buccal edge, although rather eroded, appears to have been rounded without a sharp mesiobuccal edge; the mesial enamel band is flat; and the distal enamel band is about two-thirds the width of that of M35700. In incisors of *H. nanus* and *H. quercyi*, at least, the distal enamel band narrows in a basal direction. It thus seems reasonable to suggest that M37117 represents a more basal region than M35700 (Text-fig. 40O–P).

M37116 is rather eroded but has a complete layer of cement, is a thin oval in cross section and tapers basally. It is thus considered to be a root fragment. Basally the pulp cavity is open but is reduced apically to a small lumen and must thus represent an old individual (Text-fig. 40Q–T).

M37118 is a crown fragment which differs significantly from the others (Text-fig. 40G–J). It preserves the naturally worn tip and its mesial enamel band is convex, not concave, for most of



Text-figure 40 *Heterohyus* teeth. A–F, distal views of lower preultimate molars, × 8. A, right M_1 (reversed) (UM MPR4) of *H. nanus* Teilhard from Malpérié; B, right M_2 (reversed) (UM RBN6004) of *H. nanus* from Robiac; C, left M_2 (M35709) of *H.* aff. *nanus* from Creechbarrow; D, right M_2 (reversed) (M35705) of *H. morinionensis* sp. nov. from Creechbarrow (f = facet caused by M^2 metacone); E, left $M_{1/2}$ (M35707) of *H.* cf. *sudrei* from Creechbarrow; F, right M_2 (reversed) (P. Louis collection ROB330) of *H. sudrei* Sigé from Robiac. (A, B and F drawn from casts). **G–W**, incisors of *H.* spp. indet. from Creechbarrow, × 4. G–J, ?upper right incisor crown fragment (reversed) (M37118); K–N, adapical crown fragment of lower left incisor (M35700); O–P, adbasal crown fragment of lower incisor (M37117); Q–T, root fragment of right lower incisor (reversed) (M37116); U–W, crown fragment of lower incisor (M35708). G, K, O, Q and U are distal views; H, L, P, R and V are mesial views. I, J, M, N, S, T and W are transverse sections, shown as if of left teeth and viewed basally, so that distal is to the left and mesial to the right; I, M and S are from apical ends, J, N and T from basal ends; enamel is shown as solid black and cement is delimited by a double line.

its length. It could represent a different taxon. However, the occlusobuccal angle of the worn tip is much less acute than for lower incisors (see Teilhard 1922: text-figs 40b and 41; Stehlin 1916: text-figs 340, 349; Heller 1930: pl. 5, fig. 4a–c; and Sigé 1975: text-fig. 1b–c), as it is in rodents. Also the tooth is convex mesially as in the upper incisor ('I^1?') of *Apatemys* figured by Russell *et al.* (1979: pl. 1, fig. 10). These facts support it being an upper incisor (I^1), in contrast to all the other fragments which are lowers (I_1).

Upper incisors of only two specimens of *Heterohyus* have been described and figured. One is that of the lost skull of *H. quercyi*; the other is an isolated I^1 cusp tip fragment from Mutigny (Russell *et al.* 1979: 227; pl 3, fig. 8). The latter was provisionally attributed on the basis of differences from those belonging to *Apatemys* from the same locality. Whereas the Mutigny I^1? has a complete enamel crown and is bicuspid like *Apatemys*, that of *H. quercyi* is, according to Teilhard, 'sciuroïde, émaillée sur sa face externe'. Under these circumstances, it seems unlikely that the I^1 of *H. quercyi* was bicuspid at least during most of its life. M37118 at its basal end is beginning to develop a sharp mesiobuccal edge. Like the lower incisors the enamel is slightly rugose. The worn tip is obliquely bevelled, wear being more intense mesially than distally.

If the different types of lower incisor fragment indeed represent successive segments, the minimum length for this tooth measured along the curvature would be 30 mm. A more realistic estimate, based on more gradual narrowing of the distal enamel band, would be 40 mm. From the size of the pulp cavity in M35700 compared to M37116, it is likely that the root remained open until a fairly advanced wear stage.

Order **CARNIVORA** Bowdich 1821

Superfamily **MIACOIDEA** Cope 1880
(rank emend. Simpson 1931)

Family **MIACIDAE** Cope 1880

Subfamily **MIACINAE** Cope 1880
(rank emend. Trouessart 1885)

TYPE GENUS. *Miacis* Cope 1872.

INCLUDED GENERA. *Uintacyon* Leidy 1872; *Tapocyon* Stock 1934; *Vulpavus* Marsh 1871; *Vassacyon* Matthew 1909; *Oodectes* Wortman 1901; *Paroodectes* Springhorn 1980; *Palaearctonyx* Matthew 1909; *Pleurocyon* Peterson 1919.

RANGE. Eocene, North America and Europe; Upper Oligocene, Asia?

DIAGNOSIS. See Matthew (1909: 345).

COMMENT. Miacines are generally rare in European Eocene faunas. They have been described mainly by Filhol (1876*a*), Teilhard (1915), Guth (1964), Beaumont (1966), Quinet (1968), Rich (1971) and Springhorn (1980, 1982). Flynn & Galiano (1982) have shown the Miacoidea and Miacidae to be paraphyletic, but have not resolved the interrelationships of the now caniform 'Miacinae', although they have added other genera. The old classification is thus retained as a conservative measure.

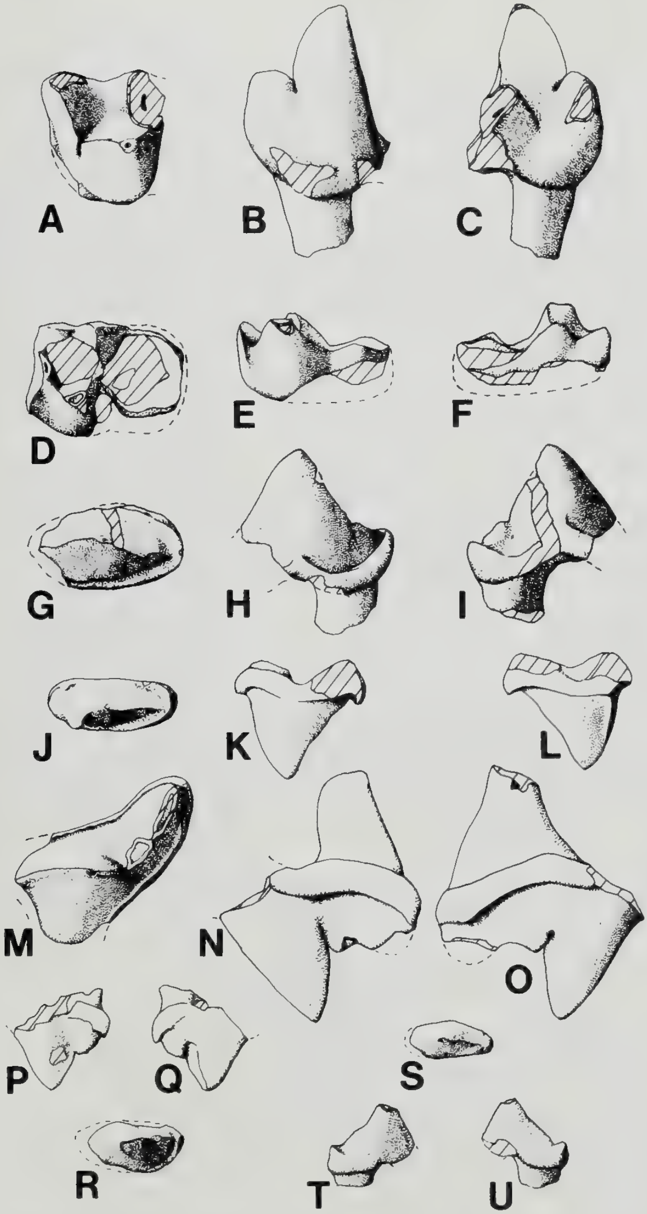
Genus *MIACIS* Cope 1873

?*Miacis* sp. indet.
(Text-fig. 41A–O)

v. *1977b* Miacidae indet.; Hooker: 141.
vp. *1980* Miacidae indet.; Hooker & Insole: 41.

MATERIAL. Right P^2 (M36206); right and left P^4s broken mesially (M36207–8); right P_4 (M36202); three left M_1 trigonid fragments (M36210–1, M37568); right M_2 (M37569).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.



Text-figure 41 Miacinae teeth. A–O, ?*Miacis* sp. indet. A–C, left M_1 trigonid fragment (M37568); D–F, right M_2 (reversed) (M37569); G–I, right P_4 (reversed) (M36202); J–L, right P^2 (reversed) (M36206); M–O, right P^4 (reversed) (M36207). P–U, Miacinae indet. P–R, Left P^3? (M36204); S–U, right P_3? (reversed) (M36200). A, D, G, J, M, R and S are occlusal views. B, E, H, K, N, P and U are buccal views. C, F, I, L, O, Q and T are lingual views. All are from Creechbarrow; × 6·6.

DESCRIPTION. The association of these few broken isolated teeth is arbitrary. The size ratios of the different tooth types fit *Miacis*, but depend on this association. The form is very similar in size to *Miacis exilis* (Filhol 1876*b*) Teilhard 1915 from the Phosphorites du Quercy.

P^2: This tooth is 2·7 mm long and 1·2 mm wide. It fits Guth's (1964: 360) description of that of *M. exilis* in the complete cingulum and its development distally into a metastyle (Text-fig. 41J–L). The preparacrista curves lingually to join the lingual cingulum halfway between the paracone and the mesial tooth margin. A faint parastyle is represented by a slight cingular swelling.

P^4: M36208 only preserves the metastylar wing. M36207 only lacks the protocone and parastyle, if there was one (Text-fig. 41M–O). The cingulum is strong and continuous and the enamel has faint wrinkles which are orientated vertically. M36207 appears to have a longer metastylar wing than do the miacine P^4s from the Sparnacian of Dormaal figured by Quinet (1968: pl. 6, figs 5–9) and also *M. exilis* (Guth 1964: pl. 15, top left fig.). It is similar to a miacine P^4 from Mormont (LGM 40937) but here the buccal cingulum is interrupted at the paracone.

P_4: This tooth is 1·8 mm wide. It is broken in the parastylid region (Text-fig. 41G–I). The cingulum appears to have been complete buccally but incomplete lingually. The small hypoconid is low and distal on the distal protoconid crest and salient only lingually; it is, however, larger than on any of the *M. exilis* P_4s figured by Teilhard (1915: 112, text-fig. 2) or by Guth (1964: pl. 15, top right fig.).

M_1: Of the three trigonid fragments, two are too corroded or broken to be worthy of description. M37568, however, is better preserved but has the metaconid broken (Text-fig. 41A–C). It is 2·7 mm wide. The buccal cingulum extends for only a short distance between the paraconid and protoconid. The paraconid has a bluntly keeled mesial edge. The distal edge of the trigonid is nearly vertical and the metaconid was probably as high or higher than the paraconid. In occlusal view the mesiolingual corner is acute, resembling in this way Guth's (1964: pl. 16) top right rather than top central figure of *M. exilis*. This feature thus appears to be of only individual significance.

M_2: This tooth is broken and corroded basally, especially round the talonid and in the trigonid and talonid basins (Text-fig. 41D–F). It nevertheless shows much lower trigonid cusps than the M_1, the paraconid and metaconid being subequal. A prominent cingular spur occurs on the mesiobuccal corner. Of Guth's (1964: pl. 16) occlusal views of *M. exilis* lower molars, in cusp pattern M37569 most closely resembles the top left figure; the other two have a more oblique arrangement. It is estimated to have been 3·2 mm long and 2·4 mm wide.

DISCUSSION. Too little is known of this form to be more precise about its affinities, but it testifies to the presence of at least one stoat-sized carnivore in the Creechbarrow fauna.

?Miacinae, gen. et sp. indet.

(Text-fig. 41P–U)

MATERIAL. Left P^3? (M36204); right P_3? (M36200).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DISCUSSION. These rather undiagnostic teeth indicate the probable presence of a second miacine in the Creechbarrow fauna, a little more than half the size of ?*Miacis* sp. indet. The left P^3? is estimated at 1·1 mm wide. The right P_3? is 0·8 mm wide.

Order **CONDYLARTHRA** Cope 1881

Family **PAROXYCLAENIDAE** Weitzel 1933

TYPE GENUS. *Paroxyclaenus* Teilhard 1922.

INCLUDED GENERA. *Kopidodon* Weitzel 1933; *Vulpavoides* Matthes 1952 (including *Russellites* Van Valen 1965); *Pugiodens* Matthes 1952 (doubtfully distinct from *Vulpavoides*); *Spaniella* Crusafont-Pairo & Russell 1967; ?*Kochictis* Kretzoi 1943.

Range. Sparnacian to Bartonian, possibly to Ludian or even to Chattian (*Kochictis*), Europe. The Asian record based on *Dulcidon* Van Valen 1965 has been removed by Tobien (1969: 30–31).

Diagnosis. See Van Valen (1965: 389).

Discussion. This small, rare, endemic European family numbers less than twenty published specimens. Fortunately three of the genera are known from skulls with nearly complete dentitions and in addition there are several skeletons from Messel. The most recent detailed studies are by Tobien (1969), Rich (1971) and Koenigswald (1983). The small number of specimens means that the degree of intraspecific variation is virtually unknown in most cases, with consequent disagreement among authors on intrageneric variation also (see below).

Van Valen's (1965, 1967) rank of family is followed here. Tobien (1969) ranked it as a subfamily of the Arctocyonidae. Ordinal affinity follows Russell & McKenna (1962) and Tobien (1969), rather than Van Valen (1965) who placed them with a query in the Insectivora. Generic content essentially follows Tobien (1969) except that *Russellites* is synonymized with *Vulpavoides*.

Genus ***VULPAVOIDES*** Matthes 1952

[incl. *Russellites* Van Valen 1965, ? = *Pugiodens* Matthes 1952]

Type species. *V. germanica* Matthes 1952. Early Lutetian, Geiseltal, D.D.R. (? = *Pugiodens mirus* Matthes 1952; see Van Valen 1965, Tobien 1969).

Included species. *V. simplicidens* (Van Valen 1965) comb. nov.; *V. cooperi* sp. nov.

Range. Early Lutetian, D.D.R.; middle Lutetian, France; late Lutetian, Switzerland; and Marinesian, England.

Emended diagnosis (modified from Van Valen, 1965: 392). Upper molars relatively short (length from 58–75% of width) with: cusps moderately high (M^1 paracone height from crown base from *c.* 90–100% of tooth length); paracone and metacone relatively close together; postmetaconule crista weak to absent; paraconule weak to absent; metaconule weak; postprotocrista confluent with metaconule; strong centrocrista not strongly indented buccally or lingually; preparaconule crista absent; ectoflexus weak to moderate. $P^{3\ 4}$ with: metacone present; and lingual half much shorter than buccal half. Note that the premolar characters are known only for the type species.

Discussion. Van Valen (1965: 390) synonymized *Vulpavoides germanica* (based on a crushed cranium with upper dentition) with *Pugiodens mirus* (based on a mandibular ramus with lower dentition) on similarity of occlusal relationships. The choice of the latter as the senior synonym was probably to avoid the suggestion of unjustified miacid relationships implied by the alternative *Vulpavoides* (i.e. like *Vulpavus*). It was unfortunate, however, as the mandible was already lost (Van Valen 1965: 391) and could not be located when I visited Halle in 1979. Tobien (1969: 28, 35) gave reasons for a certain amount of doubt regarding the synonymy of the two genera and preferred to use *Vulpavoides* as the senior synonym. If the synonymy is accepted, then Van Valen should be followed as 'first reviser' according to the ICZN rules (1985: 53). *Vulpavoides* is used here because of doubt over synonymy and the present restriction of comparisons to the upper teeth.

Van Valen (1965: 392) considered his new genus *Russellites* to be the one most closely related to *Pugiodens* (his sense), yet distinct. He later (1967: 259) synonymized it without comment with *Pugiodens*. Tobien (1969: 29) considered it distinct and to share a number of characters with *Kopidodon* not shared with *Vulpavoides*: i.e. P^4 not transversely elongated; M^2 outline identical; M^2 distobuccal corner not rounded and mesiobuccal corner projecting; M^2 buccal edge perpendicular to transverse axis; and less reduction of M^3.

However, the P^4 character based on the roots does not necessarily indicate a similarity with the very characteristic massive crown without metacone in *Kopidodon*. Also, the orientation of the buccal edge to the transverse axis shows some individual variation. In the holotype M^1 of

V. germanica it is perpendicular. In the M^1 figured by Heller (1930: pl. 1, fig. 3a–b), it is oblique, the mesiobuccal angle being obtuse. In the holotype M^1 of '*R.*' *simplicidens*, the buccal edge is perpendicular, but in NMB Bchs656 (M^1) from Bouxwiller, it is oblique, the distobuccal angle being obtuse. Furthermore the M^2 outlines in *Kopidodon* and *Russellites* are not exactly identical. The remaining characters can be more than matched by the following which are shared between *Russellites* and *Vulpavoides* but not with *Kopidodon*: upper molars with postmetacrista low, outline short and broad with paracone and metacone consequently closer together, strong centrocrista not strongly indented buccally or lingually and preparaconule crista absent.

Vulpavoides cooperi sp. nov.
(Text-fig. 42A–D, I–K)

v. *1977b* *Russellites* sp.; Hooker: 141.
v. *1980* *Pugiodens* sp.; Hooker & Insole: 42.

NAME. After Mr J. Cooper, for help with field work.

HOLOTYPE. Right M^1, M37570. Text-fig. 42A–D.

DOUBTFULLY REFERRED SPECIMEN. Left DP^4? fragment (M35646).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Small *Vulpavoides* (M^1 3·0 mm long × 5·2 mm wide); M^1 relatively short and broad (length 58% of width); with no paraconule; paracone and metacone close together; high preprotocrista joining paracone lingually; crestiform metaconule forming buccal end of postprotocrista; no postmetaconule crista; sloping height of slightly worn paracone equal to the tooth length. Ectocingulum and ectoflexus weak.

DIFFERENTIAL DIAGNOSIS. *V. germanica* Matthes is larger with stronger upper molar ectocingulum and deeper ectoflexus. *V. germanica* and *V. simplicidens* (Van Valen) have relatively longer M^1 with lower, more widely spaced paracone and metacone, cuspate paraconule and metaconule present; postmetaconule crista low; and low preprotocrista reaching only to paraconule.

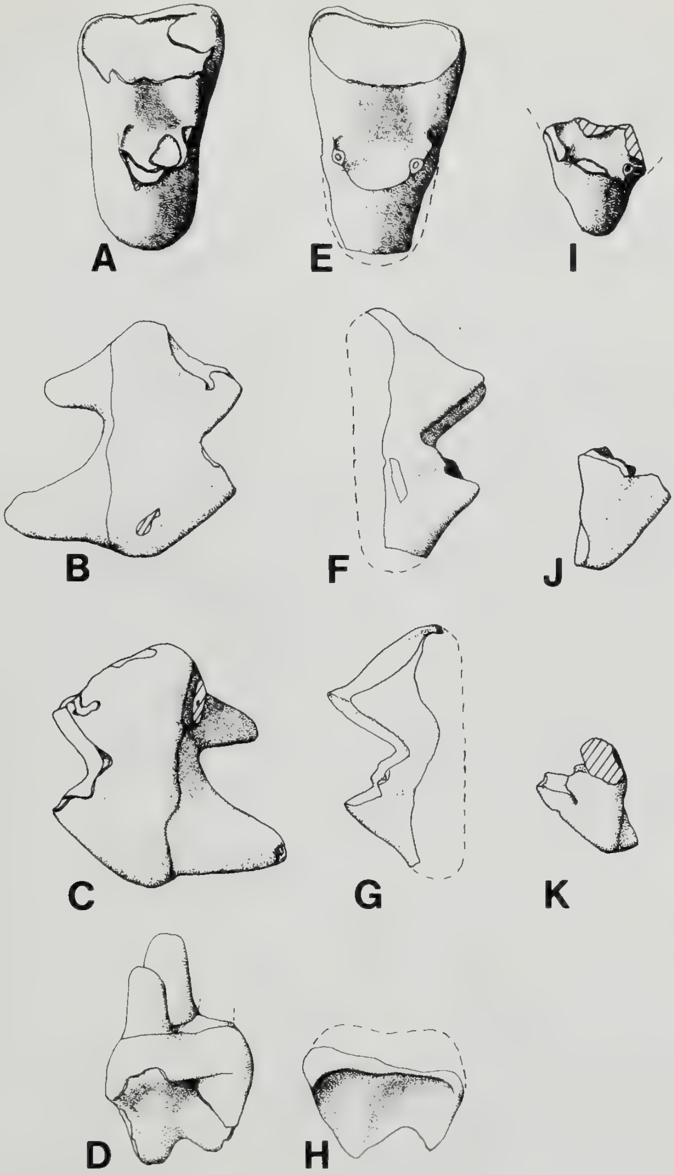
DESCRIPTION AND DISCUSSION. M37570 is considered to be an M^1 as it has an oblique buccal edge with an obtuse mesiobuccal angle. M^2s and M^3s have acute mesiobuccal angles.

There are no sharply delimited wear facets but dentine is exposed on the protocone, metaconule, paracone and metacone and also in the trigon basin and extensively over the stylar shelf, the latter merging with that on the paracone and metacone. A buccal phase facet on the distal side of the metacone suggests an angle of shear with the M_2 trigonid of about 45°. Similar smooth enamel surfaces but with no definable edges occur on the mesial side of the metacone and on both sides of the paracone.

The holotype is compared in Text-fig. 42 with the referred M^1 of *V. simplicidens* from Bouxwiller. The weak ectocingulum is similar in both and contrasts with the stronger one in *V. germanica*. The obliquity of the protocone is also like *V. simplicidens*, but M^1 of *V. germanica* is too worn to compare for this character.

One of the most striking features of M^1 of *V. cooperi* is the partial zalambdodonty. This is not so much the result of independent drawing together of the paracone and metacone, as rather an accommodation response of these cusps to extreme differential shortening of the tooth as a whole. Nevertheless, the mesocylix (the occlusal cavity within an upper molariform tooth) is very shallow buccally and must have occluded with an M_1 with a very reduced talonid. In the Eutheria, partial to complete zalambdodonty is common in palaeoryctoids, creodonts, various lipotyphlan families (see Van Valen 1966, Butler 1972), anagalids and possibly dinocerates (Matthew 1928: 970). In the Condylarthra it appears otherwise to occur in the Mesonychidae.

No milk teeth have hitherto been recorded for paroxyclaenids, but M35646 may be a DP^4 as it has relatively thinner enamel than M37570 but a somewhat similar cusp pattern (Text-fig. 42I–K). Only the lingual half is preserved, but the protocone has the same oblique orientation



Text-figure 42 *Vulpavoides* teeth. A–D, **holotype** right M^1 (reversed) (M37570) of *V. cooperi* sp. nov. from Creechbarrow. E–H, left M^1 (NMB Bchs656) of *V. simplicidens* (Van Valen) from Bouxwiller, drawn from cast. I–K, left DP^4? fragment (M35646) of *V. cooperi*? from Creechbarrow. A, E and I are occlusal views. B, F and J are mesial views. C, G and K are distal views. D and H are buccal views. All × 6·6.

and long lingual slope. It differs in the more sharply acute lingual outline, and presence of a paraconule which is buccal to the metaconule, both being isolated by clefts from the protocone. There is the faintest suggestion of a postparaconule crista.

Although only the holotype is definitely referrable to this taxon, its distinctness and the rarity of all members of the family Paroxyclaenidae are considered sufficient justification for description of a new species on an isolated M^1.

Little can be said of the relationships to the other species of the genus, but *V. simplicidens* of middle to late Lutetian age is a potential ancestor for *V. cooperi.* The minimum changes required would be molar shortening, accompanied by conule reduction and paracone and metacone height increase. *V. simplicidens* has no known specialized characters which would prevent such a relationship.

Order **CETACEA** Brisson 1762

Suborder **ARCHAEOCETI** Flower 1883

Family **DORUDONTIDAE** Miller 1923

Genus ***ZYGORHIZA*** True 1908

Zygorhiza wanklyni (Seeley 1876) Kellogg 1936

* 1876 *Zeuglodon Wanklyni* Seeley: 428–432.
v. 1907 *Zeuglodon Wanklyni* Seeley; Andrews: 124–127, fig. 1.
? *1933* *Zeuglodon wanklyni* Seeley; Burton: 161.
v. 1936 *Zygorhiza*? *wanklyni* (Seeley) ?Kellogg: 174–175.
v. 1972 *Zygorhiza wanklyni* (Seeley); Halstead & Middleton: 186–187, text-fig. 1.
v. *1980* *Zygorhiza wanklyni* (Seeley); Hooker & Insole: 41.

The history of occurrence of this whale from the Barton Clay of Barton has been fully reviewed by Halstead & Middleton (1972). In summary, the holotype skull is lost and referred material is restricted to a few isolated vertebrae. It is worthy of note that a series of about two dozen associated vertebrae is in the collections of the Bournemouth Natural Science Society. They are currently being conserved by Paul Clasby of Lymington and will be the subject of a joint project when the conservation work is finished.

Detailed stratigraphical information is not recorded with any of these specimens, but the abundance of glauconite grains on all except M12346 (figured Halstead & Middleton, 1972: text-fig. 1) strongly suggests the range of beds B–D as the provenance. M12346 may be from beds E or F as its matrix consists of non-glauconitic clay.

Family **BASILOSAURIDAE** Cope 1867

Genus ***BASILOSAURUS*** Harlan 1834

Basilosaurus sp. indet.

v. 1972 *Basilosaurus* sp. indet.; Halstead & Middleton: 187–189, text-figs 2–3.
v. *1980* *Basilosaurus* sp.; Hooker & Insole: 41.

No new specimens have come to light from the Barton Clay of Barton since Halstead & Middleton's (1972) record, but I call attention to a minor inaccuracy on p. 187 of their paper. Like most of the *Zygorhiza* specimens, the *Basilosaurus* vertebra, M26552, collected by Ken Hobby, has abundant adherent glauconite grains indicating a provenance from beds B–D, not bed E as stated. A personal communication from Mr Hobby shortly after he made the find in 1966 supports this provenance, although the specimen was not actually found *in situ* but on the slopes of Barton Cliff east of Chewton Bunny. The absence of glauconite grains from the other vertebra (M26553), collected by Paddy Blackwell, suggests a provenance of beds E–F (cf. D or E according to Halstead & Middleton, 1972: 189).

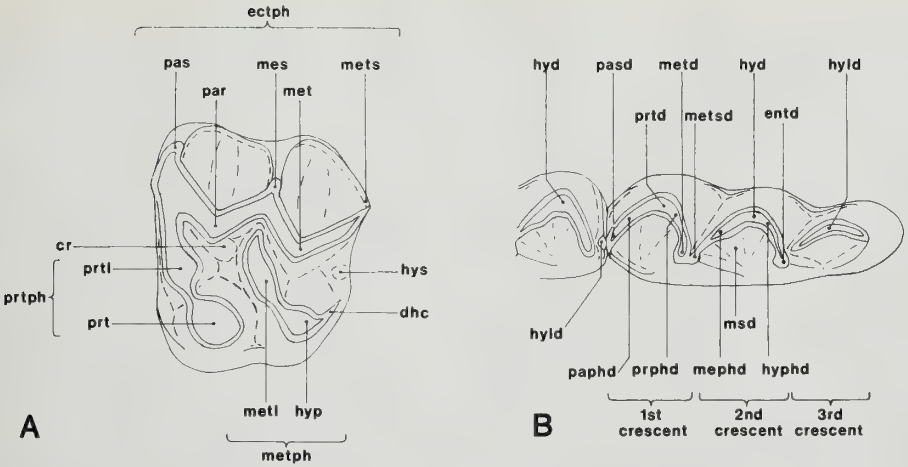
Order **PERISSODACTYLA** Owen 1848*b*

Superfamily **EQUOIDEA** Hay 1902

Family **PALAEOTHERIIDAE** Bonaparte 1850 (*sensu* Remy 1967)

TYPE GENUS. *Palaeotherium* Cuvier 1804.

INCLUDED GENERA. *Pachynolophus* Pomel 1847*a*, *Anchilophus* Gervais 1852, *Propachynolophus* Lemoine 1891, *Propalaeotherium* Gervais 1849, *Lophiotherium* Gervais 1859, *Paraplagiolophus*



Text-figure 43 Dental nomenclature of palaeotheriid cheek teeth. A, left upper molar. B, distal half of right M_2 and complete right M_3.

Abbreviations:

A. cr—rhinocerotoid crista
dhc—distal hypoconal crest
ectph—ectoloph
hyp—hypocone
hys—hypostyle
mes—mesostyle
met—metacone
metl—metaconule
metph—metaloph
mets—metastyle
par—paracone
pas—parastyle
prt—protocone
prtl—paraconule
prtph—protoloph

B. entd—entoconid
hyd—hypoconid
hyld—hypoconulid
hyphd—hypolophid
mephd—metalophid
metd—metaconid
metsd—metastylid
msd—mesoconid
paphd—paralophid
pasd—parastylid
prphd—protolophid
prtd—protoconid

Depéret 1917, *Plagiolophus* Pomel 1847*b*, *Leptolophus* Remy 1965 and *Pseudopalaeotherium* Franzen 1972.

RANGE. Late Ypresian to Stampian of Europe.

Genus ***PROPALAEOTHERIUM*** Gervais 1849

TYPE SPECIES. *Palaeotherium isselanum* Blainville 1864. Lutetian, Issel, Aude, France.

INCLUDED SPECIES. *P. helveticum* Savage, Russell & Louis 1965, *P. argentonicum* Gervais 1859, *P. rollinati* Stehlin 1905*a*, *P. hassiacum* Haupt 1925, *P. messelense* (Haupt 1925) Savage, Russell & Louis 1965, *P. parvulum* (Laurillard 1849) Depéret 1901, *P. sinense* Zdansky 1930 and ?*P. hengyangense* Young 1944.

RANGE. Early Lutetian–early Ludian?, Europe; late Eocene, China.

DIAGNOSIS. See Savage *et al.* (1965: 57).

Propalaeotherium aff. ***parvulum*** (Laurillard 1849) Depéret 1901
(Pls 20–21; Text-fig. 44A; Table 25)

v. *1977b* *Propalaeotherium* cf. *parvulum* (Laurillard 1849); Hooker: 141.
v. *1979* *Propalaeotherium* cf. *parvulum* (Laurillard 1849); Kemp *et al.*: 102.
v. *1980* *Propalaeotherium* cf. *parvulum* (Laurillard 1849); Hooker & Insole: 42.

HOLOTYPE of *P. parvulum*. This is an M^3 from the Lutetian of Argenton, Creuse, France (Blainville 1839–64: genus *Lophiodon*, pl. 3), whose 'present location [is] unknown', according to Savage *et al.* (1965: 66). Stehlin (1905*a*: 401) was also unable to locate this specimen but described and figured (1905*a*: text-fig. 25) three topotypes in Bordeaux Museum and the École des Mines, Paris (the latter now in the MNHN). Another topotype right M^3 similar to but more worn than the holotype (as figured by de Blainville) exists in the MNHN (unnumbered; cast in BM(NH) no. M42170).

MATERIAL. Right P^3 and left P^4, almost certainly associated (M36498), two P^3s (M37464, M37466), P^4 (M37465), $P^{3/4}$ (M37706), five M^3s (M35596–7, M37468–9, M37707), DP^4? in two non-fitting halves (M37467), P_2 (M37538), P_4 (M36176), five $M_{1/2}$s (M35598–9, M37470–2), M_3 (GM 978110–1; cast in BM(NH) no. M36493) and DP_2? (M37708).

HORIZONS AND LOCALITIES. The M_3 is from the Elmore Member, Barton Clay Formation, Elmore. The rest of the material is from the Creechbarrow Limestone Formation, Creechbarrow.

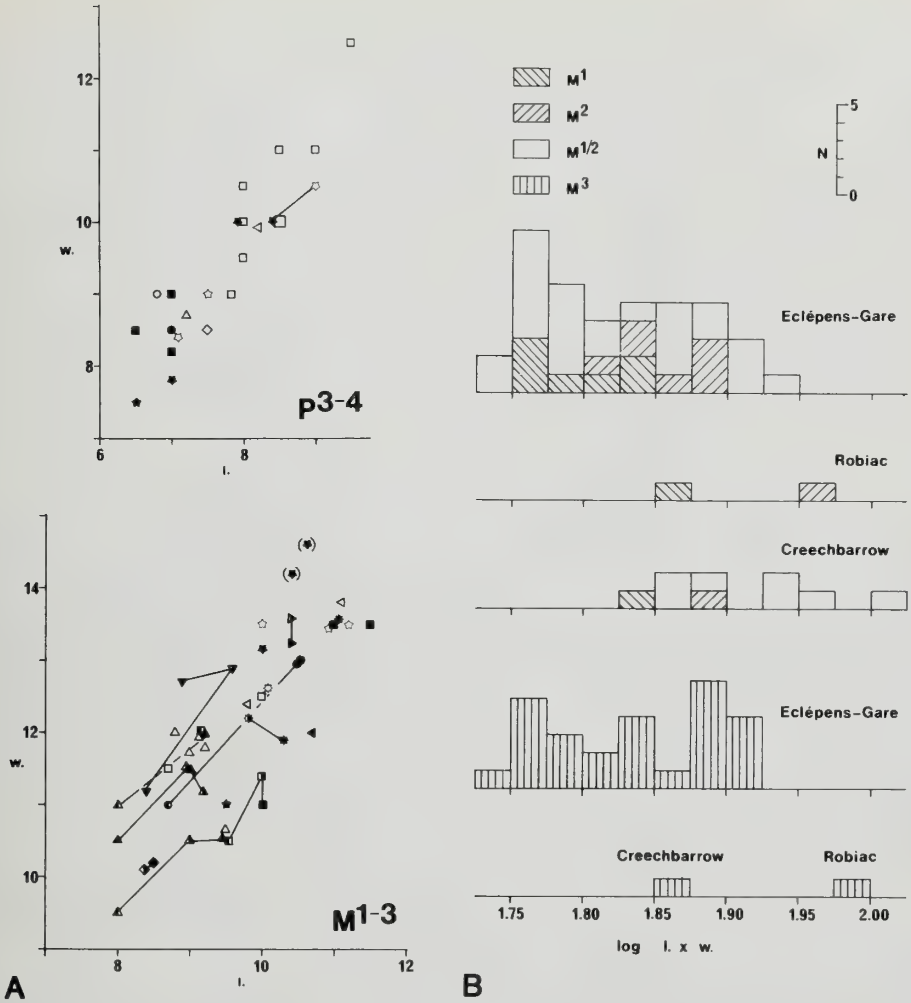
DIAGNOSIS (quoted from Savage *et al.*, 1965: 66). 'Smaller animals referable to *Propalaeotherium*, comparable in size to very large individuals of *Hyracotherium* or of *Propachynolophus maldani* (estimated skull lengths: 140 to 160 mm). Upper molars with strong and somewhat bulbous mesostyles. Protoloph and metaloph with strong posterior flexure at labial extremity giving direct connection with paracone and metacone respectively. Upper premolars non-molariform, and with no mesostyles. P_4 may have incipient entoconid; otherwise lower premolars non-molariform'.

This appears to be the most recent diagnosis of the species. However, Stehlin's (1905*a*: pl. 9) figures show that the flexure of the protoloph and metaloph is by no means a constant feature, and that the upper distal premolars can show a moderate stage of molarization with small hypocones and mesostyles. In view of the uncertainties regarding the limits and definition of *P. parvulum*, no attempt will be made here to alter the diagnosis of Savage *et al.* (1965).

AUTHORS' CONCEPT OF THE SPECIES. The name *P. parvulum* has tended to be used for all small Lutetian to Bartonian *Propalaeotherium*, not referable to *P. messelense*. Stehlin (1905*a*) frequently referred to the great variation in size and especially morphology in assemblages from Egerkingen, Chamblon and Mormont, some of which he referred to as varieties but without naming them. He (1905*a*: 430) was unable, however, to sort out these varieties into any groupings according to the different Egerkingen fissures or facies.

A study of Stehlin's (1905*a*: text-fig. 26; pl. 9) figures shows that there are quite striking differences in length/width proportions of the upper molars and distal premolars. There is also some tendency towards molarization in the case of the relatively longer P^4s (e.g. Stehlin, 1905*a*: pl. 9, figs 67, 70 in contrast with figs 1, 2, 45, 57). These differences become most marked when the material from Mormont and Creechbarrow is considered. Unfortunately these two localities have yielded few specimens.

The scatter diagrams in Text-fig. 44A are presented to show the extent of the differences in length/width proportions of P^3–M^3 from the different Egerkingen fissures and facies, and from Mormont (mainly from Stehlin's (1905*a*) measurements) and Creechbarrow (Table 25). Unfortunately there were very few measureable lower molars available to Stehlin and, whereas the majority of upper molars are from Egerkingen α, most upper premolars are from the aberrant facies. Nevertheless certain patterns seem to emerge. Upper molars of the Egerkingen γ fissure and grey marl and aberrant facies tend to be slightly larger than those from α and β fissures. Those from Mormont and Creechbarrow both plot bimodally for size and the larger specimens are relatively shorter and broader than the smaller specimens. Similarly, in the case of P^4, single specimens from α and β plot smaller than those from the grey marl and aberrant facies. The Mormont and Creechbarrow P^3s and P^4s are again bimodal but more on size and much less on proportions than are the upper molars; however, their total range is no greater than that of the aberrant facies P^4s. Two isolated $M_{1/2}$s from Creechbarrow are very similar in absolute size and proportions to those of Stehlin's (1905*b*: text-fig. 44) lower jaw (NMB Ec3), with P_{2-4}, M_{2-3}, referred to as 'Unbestimmbare Mandibularmaterialien kleiner Palaeohippiden von Egerkingen', but (1905*b*: 542) thought most likely to belong to 'einer der vielen Varietäten von



Text-figure 44 A, scatter diagrams of length (l) against width (w) of P^{3-4} and upper molars of *Propalaeotherium parvulum* (Laurillard) and *P.* aff. *parvulum* from various European localities. □ = Egerkingen grey marl facies; ○ = Egerkingen aberrant facies; ▽ = Egerkingen γ; △ = Egerkingen α; ◇ = Egerkingen β; ☆ = Eclépens-Gare; ✱ = Creechbarrow; ◁ = Lissieu; ✹ = Argenton; ▷ = Gentilly (Upper Calcaire Grossier). Of the upper premolars, solid symbols = P^3, outline symbols = P^4. Of the upper molars, symbols solid on left = M^1, on right = M^2 and completely solid = M^3; outline symbols = $M^{1/2}$. Measurements in millimetres. Lines join teeth of one individual. B, histograms of log. length × width of upper molars of *Lophiotherium siderolithicum* (Pictet) and the lectotype of *L. robiacense* Depéret, from Eclépens-Gare, Creechbarrow and Robiac. Original measurements in millimetres.

Propalaeotherium parvulum'. The lower molars of two other Egerkingen specimens (Stehlin 1905*a*: text-fig. 26; pl. 9, fig. 35) are relatively much narrower.

The greatest differences in size or length/width proportions of this material occur in the P^{3-4}s and M^3s, classically some of the intraspecifically most variable teeth (Gingerich 1974). Thus no convincing separation into two (or more) species can be made on the basis of these scatter diagrams. Until a more detailed synthesis is done of all the material (especially that from Egerkingen), it is best to accept only one species as occurring at any one time. Whether or not

Table 25 Length (l) and maximum width (w) measurements of *Propalaeotherium* aff. *parvulum* from Creechbarrow and Elmore. Measurements in millimetres.

No.	Tooth	l	w
M36498	P^3	8·4	10·0
M36498	P^4	9·0	10·5
M37464	P^3	7·9	10·0
M37466	P^3	7·0	7·8
M37465	P^4	7·1	8·4
M37707	M^3	10·0	13·2
M35596	M^3	10·6	(14·6)
M37468	M^3	10·4	(14·2)
M37538	P_2	7·2	4·3+
M36176	P_4	8·9	6·4
M35598	$M_{1/2}$	9·6	7·2
M37470	$M_{1/2}$	9·4	7·0
GM 978110–1	M_3	13·9	6·7
M37708	DP_2?	7·5	3·7

this should be considered conspecific with *P. parvulum*, based on material from the type locality, cannot be definitely decided here, hence the 'aff.' prefix to the English Bartonian specimens.

Description. Comparisons of the Creechbarrow material with the topotypes is restricted to upper molars. The Creechbarrow upper molars differ from the topotypes in having a deep fissure in the protoloph between the paraconule and protocone. This fissure is very shallow in the virtually unworn topotype $M^{1/2}$ figured by Stehlin (1905*a*: 401, text-fig. 25). It is evident from other upper molars from Argenton that the paraconule became fused to the protocone at an early wear stage. Upper molars from Eclépens-Gare (and Mormont undifferentiated, almost certainly also from Eclépens-Gare) are very similar to those from Creechbarrow in the depth of their protoloph fissure, as is the composite upper dentition from Lissieu figured by Depéret (1901: pl. 4, figs 2–3). Upper molars from Egerkingen are in general intermediate in the depth of this fissure but vary somewhat between the two extremes. Those from the younger fissures α and β appear similar in this feature to those from the older ones.

All the Creechbarrow M^3s are large and relatively short and broad, unlike the small and relatively more elongated M^3 from Mormont (Stehlin 1905*a*: pl. 9, fig. 68). Their mesostyles are also very strong.

The P^3s and P^4s can be divided into two morphological types:

	Type A	*Type B*
Outline:	Triangular	Subquadrate
Width/length ratio:	High	Low
Hypocone:	Absent	Present

In addition, type B teeth are smaller than type A teeth but not enough are available to test usefully the coefficient of variation. M37465 is fairly worn, closely resembles LM 46 from Mormont (Stehlin 1905*a*: pl. 9, fig. 67) but the hypocone appears larger; the wear makes judgement of cusp size difficult, but the remains of the lingual valley between the protocone and hypocone is nearly central on the lingual margin. M37466 is less worn, narrower lingually and with closer protocone and hypocone than M37465; unlike the latter there is also a metostyle which is distal to the midpoint of the ectoloph. Both M37465 and M37466 are type B teeth (Pl. 20, figs 1–2); the rest are type A (e.g. Pl. 20, figs 3–4).

The P_2 has no paraconid (Pl. 21, fig. 2). The metaconid is represented only by a slight lingual swelling halfway along the postprotocristid. There is a small hypoconid.

The P_4 is of roughly rectangular outline with protoconid and hypoconid in line mesiodistally (Pl. 21, fig. 3). The paralophid is weak, directed mesiolingually and dies out well buccal of the lingual margin. The entoconid is absent. In these features it is like NMB Ec3 from the Egerkingen grey marl or aberrant facies (Stehlin 1905*b*: 541, text-fig. 44). NMB Ec1 from Egerkingen α (Stehlin 1905*a*: 424, text-fig. 26) has semimolariform P_4, with a fairly large entoconid; strong convex paralophid continuous to the lingual margin; and talonid broader than trigonid.

The $M_{1/2}$s are also more like those of Ec3 than Ec1 in being relatively short and broad and in having the buccal crescents of trigonid and talonid more acute and the paralophid weaker (Pl. 21, fig. 4).

The M_3 is heavily worn. Its length/ width proportions are intermediate between those of Ec1 and Ec3. It also has an expanded hypoconulid lobe like Ec1.

The DP_2? is similar in general cusp arrangement to the non-molariform DP_2 (M35585) of *Lophiotherium siderolithicum* (see p. 352), but is longer and narrower; the talonid is lower, the entoconid being entirely missing; and the mesial slope of the metaconid is shallower, the base meeting the mesial end of the straight paralophid (Pl. 21, fig. 1).

Genus *LOPHIOTHERIUM* Gervais 1859

TYPE SPECIES. *Lophiotherium cervulum* Gervais 1859. Ludian, Euzet, Gard, France.

INCLUDED SPECIES. *L. pygmaeum* (Depéret 1901) Stehlin 1905*b* and *L. siderolithicum* (Pictet 1857) Depéret 1901 (?syn. *L. robiacense* Depéret 1917). Note that *L. magnum* Matthes 1977, *L. geiseltalensis* Matthes 1977 and *L. voigti* Matthes 1977 all appear to be synonymous with existing species of *Propalaeotherium*, but represent milk dentitions (see also Franzen 1980*b*: 91).

RANGE. Late Lutetian to Marinesian, Switzerland; Marinesian, England; Marinesian to Ludian, France; Ludian, Spain, Majorca.

DIAGNOSIS. See Savage *et al.* (1965: 72).

Lophiotherium siderolithicum (Pictet 1857) Depéret 1901
(Pl. 19, figs 8–9; Pls 22–23; Text-fig. 44B; Tables 26–27)

v. *1912* *Dictulumus leporinus* (Owen) (*sic*); Keeping: 130 (error for *Dichobunus leporinus*; in reality *Dichobune leporina* Cuvier).
v. *1977b* *Lophiotherium robiacense* Depéret; Hooker: 141.
v. *1980* *Lophiotherium robiacense* Depéret; Hooker & Insole: 42.

TYPES AND HISTORICAL BACKGROUND. Pictet (1857: 53–57; pl. 4, figs 1–3) described and figured a right maxilla with P^3–M^3 (the last tooth broken lingually) and figured (1857: pl. 4, fig. 4) an isolated worn upper right molar as representing his then new species *Hyracotherium siderolithicum*; he designated no types, so his two specimens were syntypes. Stehlin (1905*b*: 456) recognized the maxilla as the type and noted that it was lost; he did not mention the isolated molar. Following Stehlin's decision, therefore, the maxilla is recognized here as lectotype. Because it is such an advanced individual and virtually inseparable from typical maxillae in the type assemblage of *L. cervulum* from Euzet, Stehlin (1905*b*) referred it to this species. He also recognized, however, that the assemblage from Eclépens-Gare as a whole, although variable, was more primitive than typical *L. cervulum* yet more advanced than Lutetian *L. pygmaeum*. He therefore designated three phylogenetic stages A, C and E for *L. pygmaeum*, *L.* '*cervulum*' from Mormont (Eclépens-Gare) and *L. cervulum* from Euzet respectively. He thought that the mixing of the Mormont faunas (see Stehlin, 1903: 10–13) was the cause of such high morphological variation in the premolars, the type of *L. siderolithicum* thus being from a younger fauna and synonymous with *L. cervulum*. Depéret (1917) named the varieties *atavum*, *transiens* and *progressum* for individuals in the Euzet *L. cervulum* assemblage which resembled respectively Stehlin's stages A, C and E. He then gave the name *L. robiacense* to two specimens from Robiac, which he considered to represent the constant state of stage C.

Within Le Mormont, apart from a few teeth from St Loup, *L. siderolithicum* in fact is known

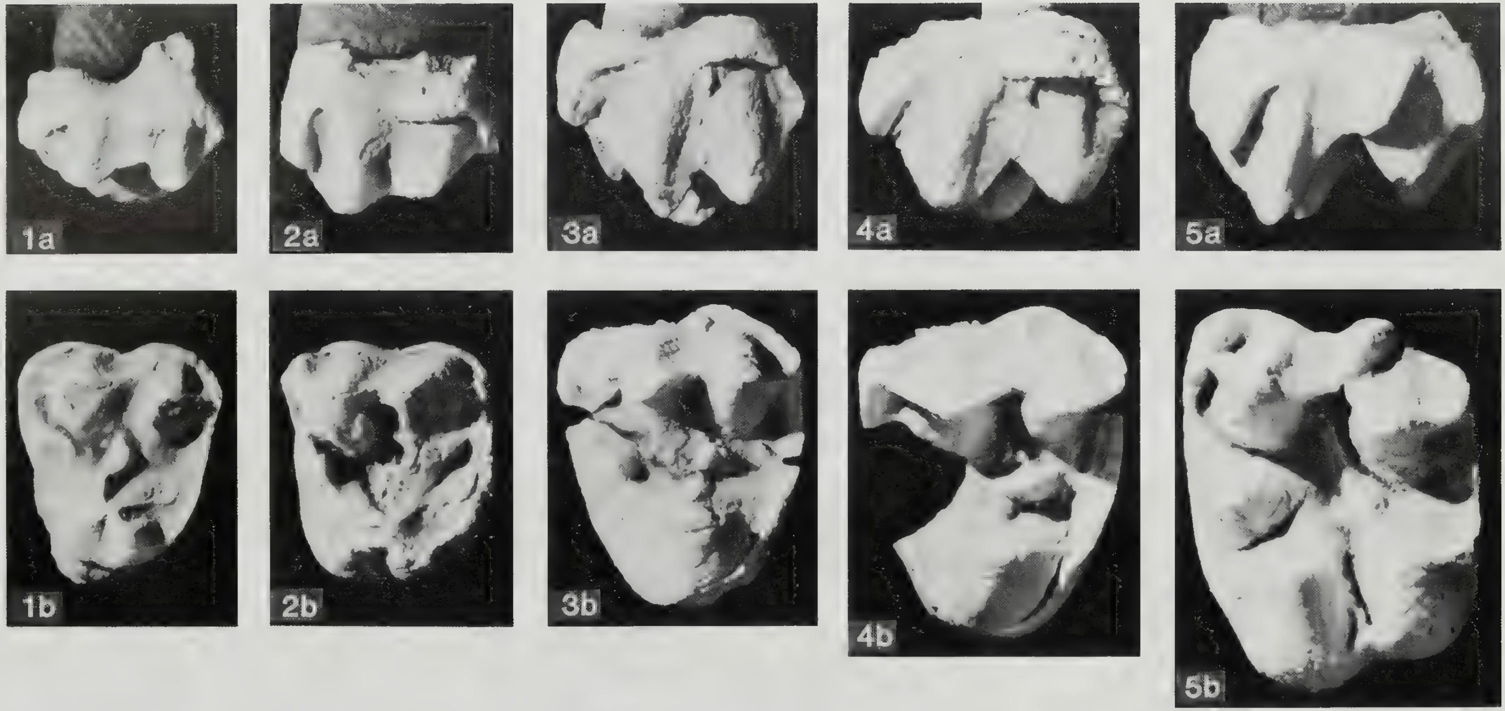


Plate 20 Light macrographs of upper cheek teeth of *Propalaeotherium* aff. *parvulum* (Laurillard) from Creechbarrow, × 4. a, buccal and b, occlusal views. Fig. 1a, b, left P^3 (M37466). Fig. 2a, b, left P^4 (M37465). Fig. 3a, b, right P^3 (reversed) (M36498). Fig. 4a, b, left P^4 (M36498, almost certainly same individual as Fig. 3). Fig. 5a, b, right M^3 (reversed) (M37707). See p. 343.

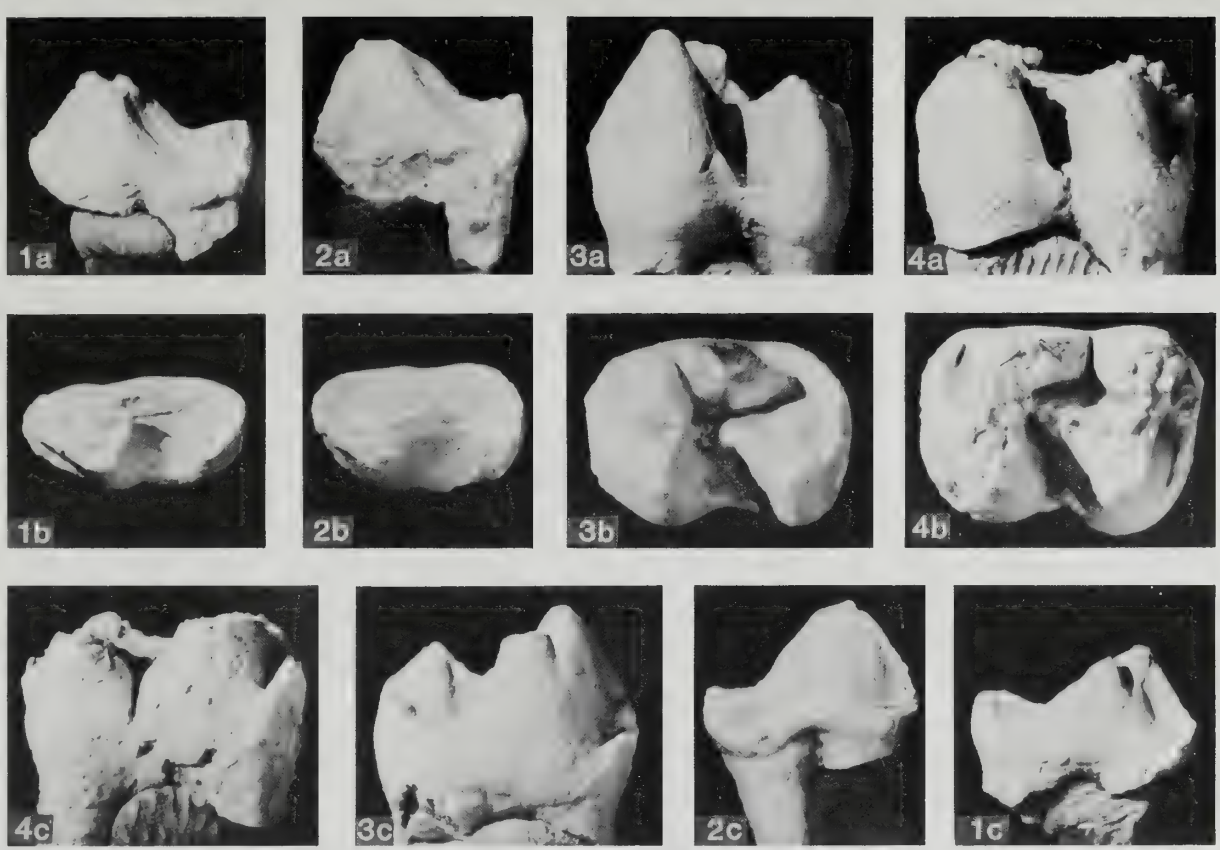


Plate 21 Light macrographs of lower cheek teeth of *Propalaeotherium* aff. *parvulum* (Laurillard) from Creechbarrow, × 4. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, left DP_2? (M37708). Fig. 2a–c, right P_2 (reversed) (M37538). Fig. 3a–c, left P_4 (M36176). Fig. 4a–c, left $M_{1/2}$ (M35598). See p. 343.

only from Eclépens, associated with an almost exclusively Marinesian mammal fauna (see Hartenberger, 1973: 68, for list), and de la Harpe (1869: 459) noted that out of five or six fissures in the quarry at Gare d'Eclépens, almost all of the animal fossils came from a single fissure. The degree of size variation is low (see Text-fig. 44B), supporting the idea that the old collections of Eclépens *L. siderolithicum* constitute essentially a single assemblage. Thus the high morphological variation recorded by Stehlin for the premolars of *L. siderolithicum* is considered to be an accurate representation of the species. The position is, however, unfortunately complicated in that other fissures were exploited after the time of de la Harpe and the specimens were not differentiated in the LGM collections (M. Weidmann, personal communication 1983).

The species name does not appear to have been used in major zoological literature since Depéret (1917). Savage *et al.* (1965) did not even include it in a synonymy list, considering that the Mormont material probably belonged to *L. robiacense*. They nevertheless doubted the constancy of the premolars of *L. robiacense*, the species being represented at most by two specimens. Sudre (1969*a*: 103–105, 118) pointed out that both specimens came from a very high level in the Robiac section which Roman (1904) considered to be lowest Ludian. As such, they are likely to be little older than the specimen from Fons 1 figured by Remy (1967) as *L.* aff. *cervulum*.

Remy (1967: 29–30) decided that species of *Lophiotherium* could only be determined on tooth morphology by statistical procedures, individual specimens being useless. He then showed that *L. pygmaeum*, *L. robiacense* and *L. cervulum* could be distinguished by P^{1-4}/M^{1-3} length ratio with no overlap. However, he was only able to measure one specimen of each of *L. pygmaeum* and *L. robiacense*; and the former is composite (Stehlin 1905*b*: 452, text-fig. 31).

It is considered here that the best procedure is to recognize *L. siderolithicum* as a statistically well-represented species, the type assemblage being essentially homogeneous, and a senior synonym of *L. robiacense* (if the two are identical).

MATERIAL. (54): Associated left P^4–M^2 (M36177); two P^1s (M37410–1); P^2 (M36497); two P^3s (M37412, M37703); two P^4s (M37413–4); twelve $M^{1/2}$s (SMC 9969, M35584, M36499,

Table 26 Length (l) and maximum width (w) measurements of *Lophiotherium siderolithicum* from Creechbarrow. Measurements in millimetres.

No.	Tooth	l	w	No.	Tooth	l	w
M37410	P^1	5·4	4·4	M37430	P_4	7·7	5·7
M36497	P^2	4·1	–	M37705	P_4	7·3	5·9
M37703	P^3	–	8·0	M37705	M_2	7·8	6·2
M37413	P^4	7·5	9·7	M37431	$M_{1/2}$	–	5·5
M36177	P^4	7·0	9·7	M37432	$M_{1/2}$	7·8	5·9
M36177	M^1	7·1	9·9	M37433	$M_{1/2}$	8·2	5·5
M36177	M^2	7·2	10·7	M37434	$M_{1/2}$	7·6	6·1
M35584	$M^{1/2}$	7·5	–	M37436	$M_{1/2}$	8·0	5·4
M37415	$M^{1/2}$	7·4	9·8	M35587	$M_{1/2}$	(7·3)	5·5
M37416	$M^{1/2}$	8·1	10·6	M37705	M_3	11·0	6·3
M37417	$M^{1/2}$	7·8	10·9	M37438	M_3	10·5	5·6
M37418	$M^{1/2}$	7·6	9·7	M37440	M_3	–	6·1
M37419	$M^{1/2}$	8·7	11·9	M37441	M_3	(11·0)	5·7
M37421	$M^{1/2}$	8·5	10·8	M37442	M_3	(11·0)	5·8
C9969	$M^{1/2}$	7·6	10·3	M36180	M_3	10·5	5·5
M36178	M^3	7·0	10·3	M35585	DP_2	6·6	4·1
M37424	M^3	–	10·6+	M35590	DP_3	–	4·5
M37426	DP^3	7·4	7·2	M37447	DP_3	7·4	5·0
M37427	DP^4	7·6	9·1	M37449	DP_3	–	5·6
M37428	DP^4	6·5	7·6	M35586	DP_3	7·6	5·0
M35588	P_4	7·0	5·3	M37451	DP_4	6·9	5·3
M37429	P_4	7·1	5·1	M37452	DP_4	7·7	5·3

M37415–23); three M^3s (M36178, M37424–5); upper molar fragment (M36179); DP^3 (M37426); three DP^4s (M37427–8, M37704); associated left P_4, $M_{2\ 3}$ (M37705); five P_4s (M35588, M35594, M37429–31); eight $M_{1/2}$s (M35587, M35589, M37432–7); eight M_3s (M36180, M37438–44); two lower molar fragments (M35591, M37445); two DP_2s (M35585, M37446); six DP_3s (M35586, M35590, M37447–50); four DP_4s (M35592–3, M37451–2); lower canine (M36828).

DOUBTFULLY REFERRED MATERIAL. (23): Two upper canines (M37453–4); twenty one incisors (M35595, M36228–35, M36237–8, M36792, M37455–63).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS (modified from Savage *et al.* (1965: 79–80) for *L. robiacense*). Molariform upper teeth with very strong and discrete paraconules, weak to strong, indistinct to discrete metaconules; P^4 hypocone missing to as developed as protocone, usually moderately to well developed; P^3 hypocone missing or of height equal to protocone, poorly to well separated from it, usually moderately separated; P^2 hypocone missing or of height equal to protocone, poorly to moderately separated from it. P_4 entoconid moderately to strongly developed; P_3 entoconid weak to moderate; P_2 metaconid weak to strong.

DESCRIPTION. In tooth size the Creechbarrow assemblage is slightly larger than the Eclépens-Gare assemblage (see Text-fig. 44B) but there is much overlap. In morphology the two are very similar (Table 27), the latter having been described in detail by Stehlin (1905*b*).

In response to Remy's (1967) comments (see p. 350) I have attempted to divide into categories the grades of molariformity of the upper (those with the greatest number of easily recognizeable character states) premolars and score numbers of individual teeth for both assemblages. The different premolars are mainly isolated and often difficult to distinguish from one another. It seems possible to distinguish P^4s from P^3s because the latter have smaller, more mesial metaconules and are smaller overall. Moreover, they molarize differently: in P^4 the hypocone 'grows' gradually on the postprotocingulum, some distance behind the protocone, moving further distally in advanced stages; in P^3 the hypocone, from its moment of appearance, is the same height as the protocone and progressively buds off distally from it. P^2s molarize like P^3s and are difficult to separate except on smaller size and narrower proportions. P^1 is a small narrow wedge-shaped tooth with poorly differentiated protocone and hypocone. In Table 27, the number of specimens from both Eclépens-Gare and Creechbarrow and the lectotype of *L. robiacense* from Robiac are shown for each category of the four upper premolars. Although the peaks of the Creechbarrow character state distributions do not always correspond to those of Eclépens-Gare, they are not so skewed to one or other end of the scale as they are in *L. cervulum* or *L. pygmaeum*.

The isolated upper deciduous premolars (Pl. 22, figs 5–6) are identified as DP^3 and DP^4 and resemble those figured by Stehlin (1905*b*: 459, text-fig. 36) from Eclépens-Gare.

The lower cheek teeth from Creechbarrow also closely resemble those of the Eclépens-Gare assemblage, being only slightly larger (see Table 26 for measurements). Recognizing the different isolated lower premolars is difficult. Moreover, the fully molariform P_4s are very like M_1s or M_2s. Three molariform teeth from the left side of the jaw, from Hole 6 at Creechbarrow (Text-fig. 4, p. 209), have identical preservation and very similar wear states (Pl. 19, fig. 8). One is M_3; an M_2 can be associated with it by matching up interstitial facets; the third does not fit against the M_2 but is almost certainly from the same individual. Its hypolophid is weaker than that of M_2 and its entoconid, although well developed, is slightly lower than the metaconid. It is thus identified as P_4 and is as fully molariform as that of *L. cervulum* figured by Savage *et al.* (1965: 74, text-fig. 35c–d). Of three isolated teeth, identified as P_4, one is fully molariform like the Hole 6 one; another is worn but would have had the entoconid little more than half the height of the metaconid (Pl. 23, fig. 4); and a third is intermediate between the two.

Lower deciduous premolars are also difficult to separate from one another when isolated. Those here identified as DP_3 and DP_4 (e.g. Pl. 23, figs 2–3) are very similar to those figured by Stehlin (1905*b*: 469, text-fig. 39). An unworn non-molariform tooth with thin enamel and a

Table 27 Numbers of specimens in each character state of the four upper premolars, for assemblages of *Lophiotherium* at Eclépens-Gare and Creechbarrow. At right, condition in the lectotype of *L. robiacense* from Robiac.

Tooth	Category	Eclépens-Gare	Creech-barrow	Robiac
P^4	1. Hypocone undifferentiated on postprotocingulum	3	0	
	2. Hypocone very small on postprotocingulum	3	0	
	3. Hypocone smaller than protocone, postprotocingulum broken	8	0	1
	4. Hypocone = protocone, closer than paraconule to metaconule	3	2	
	5. Hypocone = protocone, same distance apart as paraconule and metaconule	6	1	
P^3	1. Hypocone undifferentiated on postprotocingulum	3	0	1
	2. Hypocone very close to protocone	7	1	
	3. Hypocone closer to protocone than paraconule to metaconule	9	1	
	4. Hypocone–protocone distance = paraconule–metaconule distance	4	0	
P^2	1.	5	0	1
	2. Same numbered categories as for P^3	4	1	
	3.	5	0	
P^1	1. Metacone absent	2	0	
	2. Metacone small	4	0	
	3. Metacone subequal with paracone	0	1	1

papillate buccal cingulum between protoconid and hypoconid (M35585) is tentatively identified as DP_2. Its metaconid and metastylid are scarcely separated even at the tip, the entoconid is very small and mesial and distal parts are of approximately equal width (Pl. 23, fig. 1). As DP_2 it thus resembles *L. pygmaeum* more than it does *L. siderolithicum* as figured by Stehlin (1905*b*: 469, text-figs 38–39), and contrasts strongly with a more typical Creechbarrow DP_2 (M37446).

A palaeotherioid curved lower canine with a distal facet (M36828) (Pl. 19, fig. 9) resembles those of *L. cervulum* figured by Depéret (1917: pl. 15). It is of appropriate size to belong to *L. siderolithicum*. While attempting to identify miscellaneous canines from Creechbarrow, I noticed a strong resemblance between M36828 and the isolated canines described from Egerkingen and Mormont as *Choeromorus jurensis* Stehlin 1908 and *C. helveticus* Pictet & Humbert 1869 (particularly Pictet & Humbert 1869: pl. 25, fig. 11a). Because of their resemblance to miniature pig canines, these authors assumed that they were congeneric with the contemporary genus *Cebochoerus*, which was based on cheek teeth, and at that time placed in the family Suidae (now Cebochoeridae, p. 389). An anomaly was caused by the knowledge of certain tooth rows with typical *Cebochoerus* cheek teeth associated with non-*Choeromorus*-like canines. Stehlin 'resolved' the problem by assuming that the genera *Cebochoerus* and *Choeromorus* could only be distinguished on the canines as they had identical cheek teeth. Sudre (1978*b*: 52–54) discussed the problem in more detail and considered two other possible solutions: either that the canines of *Cebochoerus* were sexually dimorphic or that the canines attributed to *Choeromorus* belonged to another kind of animal. They have never been found *in situ* in a jaw with a *Cebochoerus* cheek dentition, so Sudre's second solution seems the more likely. In fact a close resemblance exists between Stehlin's (1908: 708, text-figs 101–102) two crucial specimens and the lower canines of *Anchilophus* cf. *dumasii* figured by Remy (1967: 23, text-fig. 13; pl. 5, fig. 1). *Anchilophus* occurs in both the Egerkingen and Mormont faunas identified on cheek teeth and generic identity of the canines with these seems very likely. The strong pig-like curvature to these teeth was evidently to overcome accommodation problems in the long, shallow mandibular symphyses of both *Lophiotherium* and *Anchilophus*.

Two upper palaeotherioid canines of appropriate size and proportions are tentatively attributed to *L. siderolithicum*, as are various incisors which resemble those in Depéret's figures of *L. cervulum* (1917: pl. 15, fig. 9).

Conclusions. The presence of *L. siderolithicum* at Creechbarrow is good evidence of later Bartonian age. Its slightly larger size compared to the type assemblage might indicate either geographical differences or a temporal trend towards the even larger specimens from Robiac. There is no independent evidence either way, but the *Lophiotherium* lineage appears to have undergone no significant or directional change in size throughout its known stratigraphical range.

Genus ***PLAGIOLOPHUS*** Pomel 1847*b*
[= *Paloplotherium* Owen 1848*a*]

Type species. *Palaeotherium minus* Cuvier 1804. Première Masse du Gypse, Montmartre, Paris, France.

Included species. *P. cartieri* Stehlin 1904*b*, *P. lugdunensis* (Depéret & Carrière 1901), *P. cartailhaci* Stehlin 1904*a*, *P. annectens* (Owen 1848*a*), *P. fraasi* Meyer 1852, *P. javalii* (Filhol 1877*b*) (doubtfully distinct from *P. fraasi*) and *P. curtisi* sp. nov.

Range. Late Lutetian–Stampian, Europe.

Emended diagnosis (modified from Viret (1958: 359) and largely complementing Franzen's (1968: 16) diagnosis of *Palaeotherium*). Medium–small to medium–large Palaeotheriidae, cranium length 150–300 mm. DP^1 replaced by P^1 or both absent. Cheek teeth with or without cement; with high percentage of pericanalicular dentine (Remy 1976); and semihypsodont. Upper molars with buccal cusp height from 70–100% of tooth width and from 1·3–1·6 times the lingual cusp height. Upper molariform cheek teeth with prominent paraconules and high oblique metalophs. P^3 with or without metacone and without hypocone; P^4 with or without elongate metaloph and without hypocone; P_3 with or without hypoconid and without entoconid; P_4 with or without small entoconid and with high hypoconid. Successive molars increase in size distally. Lower cheek teeth with weak interrupted buccal cingulum; and lingual valley of first crescent deep. M_{1-2} with hypoconulid. Twinned metaconid/metastylid on molariform lower cheek teeth. Postcanine diastema medium short to medium long (lowers from 29–36% of cheek tooth row; uppers from 15–26% of cheek tooth row). Narial incision varying in depth from P^1 to M^1, the lower border consisting of premaxillae plus maxillae. Astragalus trochlear ridges at angle of 75° to navicular facet.

Plagiolophus curtisi sp. nov.

For type material, see under nominate subspecies. For synonymy, see under each subspecies.

Diagnosis. 1, small to medium-sized *Plagiolophus* (M^2 length 13·0–16·5 mm); 2, tooth cement absent; 3, P^1 present; 4, P^3 metacone present; 5, P^4 metaloph short, not reaching distal cingulum; 6, $P^{3\ 4}$ metaloph nearly longitudinally orientated; 7, $M^{1\ 2}$ distal hypoconal crest strong and longitudinally orientated; 8, upper cheek teeth with high distal cingulum; 9, upper molar paracone and metacone buccally salient; 10, upper molar metaloph obliquity medium; 11, molar crown height medium (height of buccal cusps $\simeq$ maximum width of tooth); 12, upper molar buccal/lingual height ratio low; 13, upper molar protoloph fissure between paraconule and protocone moderately deep; 14, upper molar 'rhinocerotoid' crista present; 15, $M\frac{3}{3}$ moderately distally expanded; 16, canines large and parallel orientated; 17, P_3 hypoconid present; 18, P_4 entoconid absent; 19, lower molar buccal/lingual height ratio 1 : 1; 20, molar enlargement gradient low. Muzzle broad anteriorly and mandibular symphysis narrow; palatal concavity

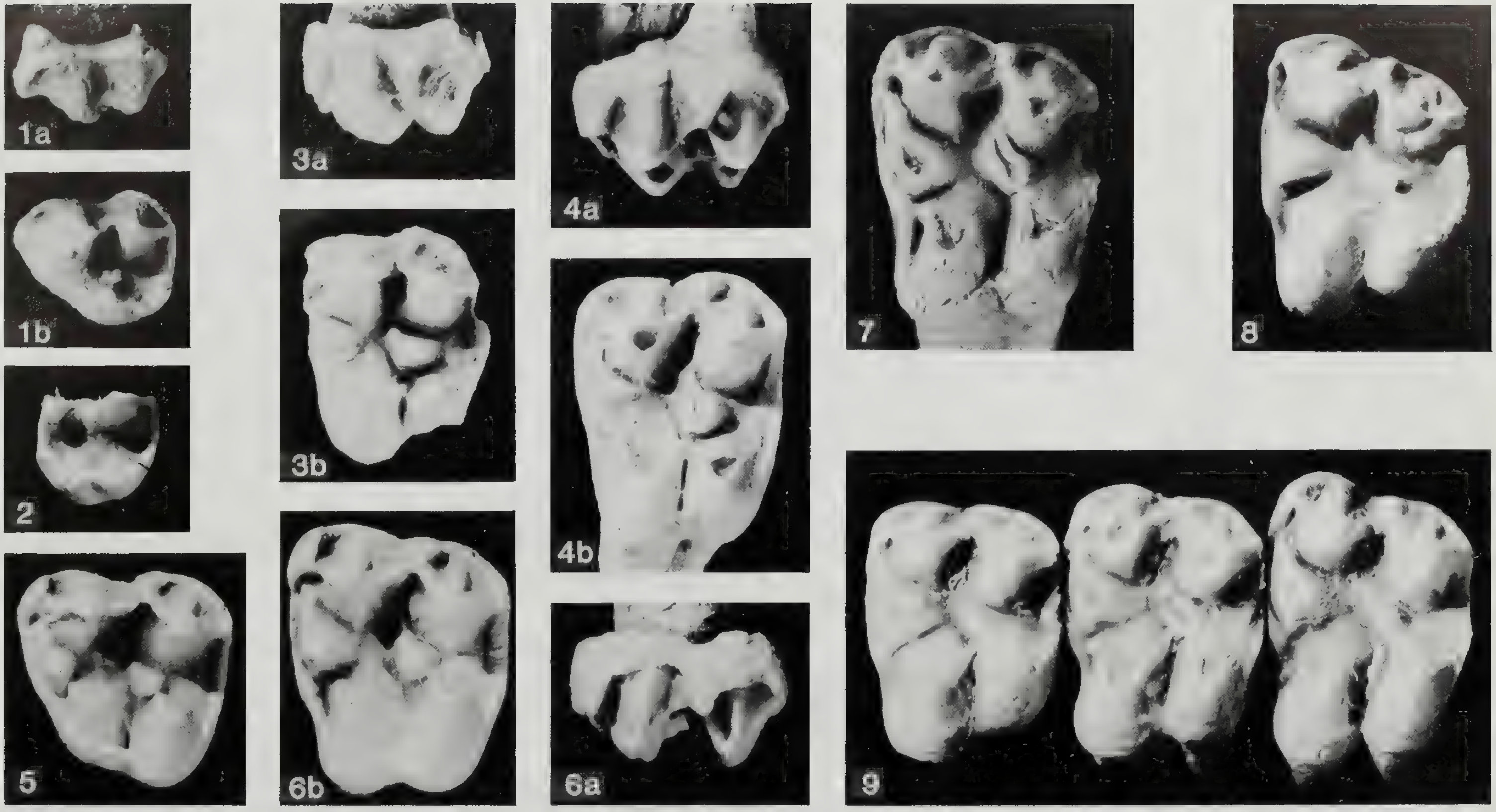


Plate 22 Light macrographs of upper cheek teeth of *Lophiotherium siderolithicum* (Pictet) from Creechbarrow, × 4. Views are buccal (a) and occlusal (b and unsuffixed). Fig. 1a, b, right P^1 (reversed) (M37410). Fig. 2, left P^2 (M36497). Fig. 3a, b, right P^3 (reversed) (M37703). Fig. 4a, b, left P^4 (M37413). Fig. 5, left DP^3 (M37426). Fig. 6a, b, left DP^4 (M37427). Fig. 7, left $M^{1/2}$ (SMC 9969). Fig. 8, right M^3 (reversed) (M36178). Fig. 9, left P^4–M^2 (M36177). See p. 347.

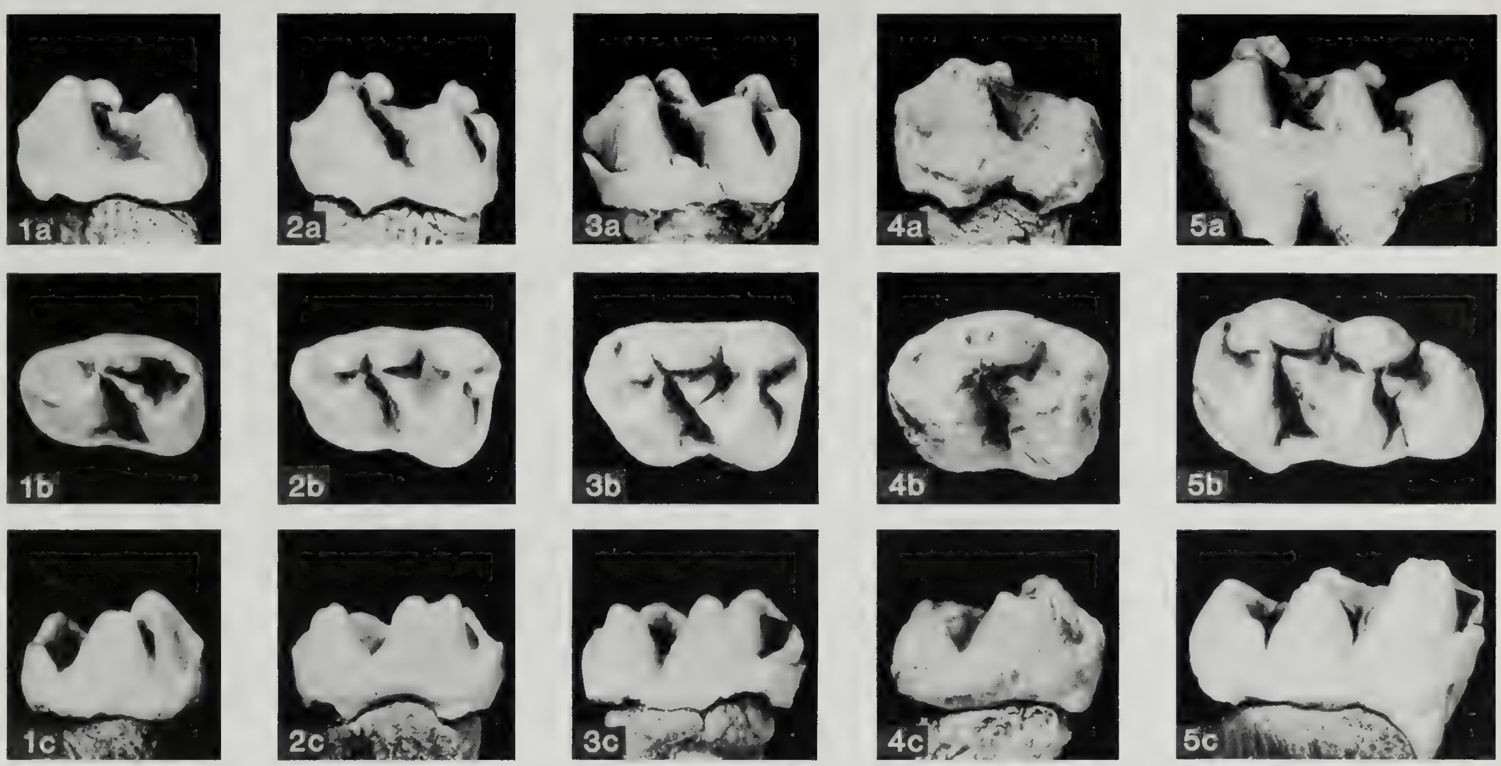
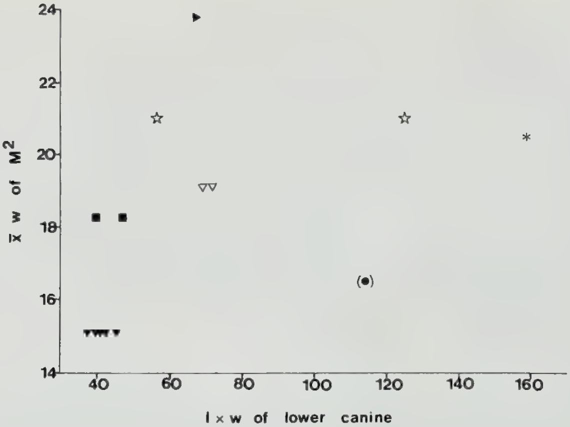

1a
2a
3a
4a
5a
1b
2b
3b
4b
5b
1c
2c
3c
4c
5c

Plate 23 Light macrographs of lower cheek teeth of *Lophiotherium siderolithicum* (Pictet) from Creechbarrow, × 4. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, left DP_2 (M35585). Fig. 2a–c, left DP_3 (M37447). Fig. 3a–c, right DP_4 (reversed) (M37452). Fig. 4a–c, left P_4 (M37430). Fig. 5a–c, left M_3 (M37438). See p. 347.



Text-figure 45 Scatter diagram of length × width of lower canine against mean width of M^2 of *Plagiolophus* and *Paraplagiolophus*. Measurements in millimetres. ■ = *Plagiolophus annectens* (Owen) from Hordle Cliff; ▼ = *P. minor* (Cuvier) from La Débruge; ▶ = *P. fraasi* Meyer from the Phosphorites du Quercy; ▽ = *P.* sp. from Egerkingen γ; ∗ = *P. curtisi curtisi* sp. & subsp. nov. from Barton Cliff; ● = *P. curtisi creechensis* subsp. nov. from Creechbarrow; ☆ = *Paraplagiolophus codiciensis* (Gaudry) from Jumencourt (Upper Calcaire Grossier).

shallow between diastemata; frontal region flat with supraorbital rims and postorbital processes thin and horizontal; ascending mandibular ramus posteriorly expanded. (Note that the non-dental characters are only known for the nominate subspecies. Dental characters are numbered for later discussion).

Plagiolophus curtisi curtisi subsp. nov.

(Pl. 24, figs 1–2; Pl. 25; Pl. 26, fig. 4; Text-figs 45, 46, 47A, 48A–C, 49B, 50C–D, 51; Table 28)

v. *1972* *Plagiolophus cartailhaci* Stehlin; Hooker: 180–182.
v. *1980* *Plagiolophus* sp. 2; Hooker & Insole: 42.

NAME. After Mr R. J. Curtis, who found the only known specimens.

HOLOTYPE. Very fragmentary associated cranium and mandible (M26176) consisting of 15 non-fitting pieces: palatal fragment with ventral parts of canine alveoli, root and alveoli of left P^1 and mesial part of lingual root of left P^2; left maxillary fragment with distal root parts of P^2 and P^3–M^3 with crowns; right maxillary fragment with M^{1-3} and part of orbital floor; left and right glenoid regions; fragment of left frontal; mandibular symphysis with roots of right I_1–C and left $I_{1\ 2}$ and C (right C with fragment of crown); left horizontal mandibular fragment, with distal root of P_3, P_4 and M_2 with crown, roots of M_1; talonid and hypoconulid of left M_3; fragment of left ascending ramus; right horizontal mandibular fragment with distal root of P_4 and M_{1-3} with crowns; fragment of right ascending ramus; fragment of right coronid process; right mandibular condyle; and an undetermined bone fragment. The buccal surfaces of many of the teeth have been eroded, presumably following exposure in the field.

PARATYPE. Right M^3 (M26238).

TYPE HORIZON AND LOCALITY. Proximity of junction of Beds D and E, Barton Clay Formation, Barton Cliff at Barton-on-Sea. From the wave-washed lower part of the cliff at about SZ 236928.

DOUBTFULLY REFERRED MATERIAL. Proximal half of right radius (M34864) from the Barton Clay Formation, Barton Cliff, not *in situ*, but preservation suggesting derivation from around Bed E.

DIAGNOSIS. 1, large (M^2 length 16·5 mm); 2, P^{3-4} protocones mesiodistally elongated; 3, upper molar metaloph without metaconule; 4, subterminal metastyle present.

Table 28 Length (l) and maximum width (w) measurements of *Plagiolophus curtisi* from Creechbarrow and Barton. Measurements in millimetres.

No.	Tooth	l	w	No.	Tooth	l	w
M36181	C^1	(10·7)	–	M36181	C_1	12·0	(9·5)
M37473	C^1	9·3	7·3	M26176	C_1	14·8	10·8
M36181	P^2	6·6	9·8	M36181	P_2	8·5	5·3
M37474	P^2	7·0	9·4	M37484	P_2	–	4·1
M37475	P^2	7·3	–	M36181	P_3	8·6	6·8
M36181	P^3	7·9	12·3	M36182	P_3	7·0	5·0
M37476	P^3	8·3	–	M37485	P_3	7·6	5·4
M26176	P^3	10·5	(13·0)	M36181	P_4	9·9	8·1
M36181	P^4	9·3	14·3	M26176	P_4	12·0	(9·0)
M37479	P^4	(9·4)	–	M36181	M_1	(11·5)	7·9
M26176	P^4	12·3	(15·7)	M26176	M_1	14·3	(9·4)
M36181	M^1	10·3	(15·7)	M36181	M_2	13·0	9·4
M26176	M^1	14·4	(19·5)	M26176	M_2	15·4	11·2
M36181	M^2	13·0	16·5	M37486	$M_{1/2}$	10·7	7·4
M26176	M^2	16·5	(20·2)	M37487	$M_{1/2}$	–	7·9
M36181	M^3	18·7	18·2	M36181	M_3	20·0	8·9
M26176	M^3	23·9	20·3	M37709	M_3	–	8·7
M26238	M^3	20·0	20·6	M26176	M_3	23·3	10·4

DESCRIPTION. *Canines*: The remains of the posteroventral alveolar walls of the upper canines indicate massive roots, once extending at least to the level of P^1 (Pl. 24, figs 1a, d). Viewed dorsally they are parallel and laterally they are at an angle of 20–30° to the diastematal ridges. X-rays of an *in situ* upper canine of *P. fraasi* (M1880) show a corresponding angle of *c.* 40° (Pl. 24, fig. 3). Judged from the muzzle shape, the root apices must converge posterodorsally in this and other species of the genus.

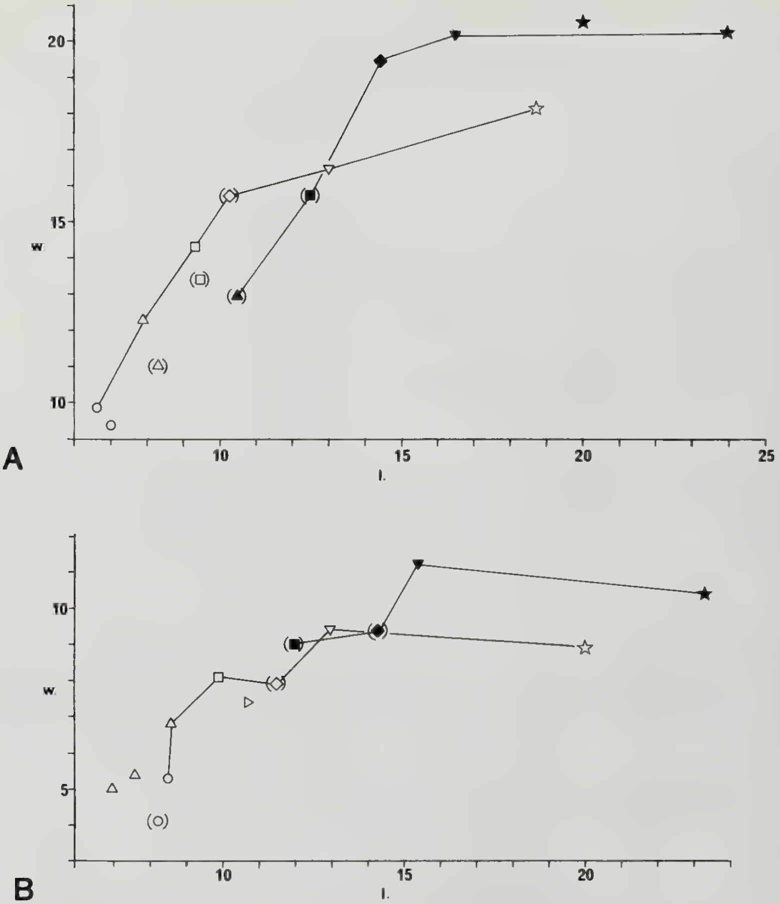
The lower canines of M26176 have similar size and orientation to the uppers but lie closer together; the roots extend to the posterior limit of the symphysis (Pl. 26, fig. 4). X-rays of *P. annectens* and *P. minor* show short convergent roots which terminate posteriorly well in front of the end of the symphysis, despite slight age variation (Pl. 26, figs 2–3). Symphysial shape in the other species indicates similarity to *P. annectens.*

Canine size is compared in Text-fig. 45 with that of other *Plagiolophus* species, in which they are always relatively smaller. The possibility of sexual dimorphism in this feature must be considered (see Stehlin 1905*a*: 330; Depéret 1917: 46). Slight bimodality has been demonstrated for one species of *Palaeotherium* (Franzen 1968: 133) but a similar exercise has not been attempted for *Plagiolophus.* The examination of much material in various European museums has not shown any individuals with canines as large as those of M26176. Their occurrence in more than one individual at Creechbarrow is further support for canine size as a taxonomic character, whether or not it may eventually turn out to be dimorphic in this species.

Upper premolars: P^1 is interpreted as having had three roots, being represented now by a lingual root, a distobuccal alveolus and an eroded or partially resorbed mesiobuccal alveolus. The tooth may thus have been very worn and about to fall out.

The roots of P^2 in spanning two non-fitting bone fragments guide reconstruction in this area (see Text-fig. 51, p. 366).

On P^3 there is evidence of a metacone, despite the buccal erosion and heavy wear, since there appear to be two lingual bulges from the remains of the ectoloph and the paracone has a mesial position. The paraconule is distinct on the protoloph. The complete edges of the tooth have a continuous cingulum, which distally forms a high ridge. Heavy wear has fused this ridge to the metaloph and ectoloph but it is still separated from the protocone by a valley. The metaloph is fused distally to the ectoloph whilst mesially it is terminated by minor buccal and lingual crests, the last joining the protocone.



Text-figure 46 Scatter diagram of length (l) against width (w) of (A) upper and (B) lower cheek teeth of *Plagiolophus curtisi curtisi* sp. & subsp. nov. from Barton Cliff (solid symbols), and *P. curtisi creechensis* subsp. nov. from Creechbarrow (outline symbols). Measurements in millimetres. ○ = P^2_2; △ = P^3_3; □ = P^4_4; ◇ = M^1_1; ▽ = M^2_2; ☆ = M^3_3; ▷ = $M_{1/2}$. Lines join teeth of one individual.

P^4 is similar to P^3 but the paracone and metacone seem better separated. The metaloph has similar mesial crests to P^3 and bends at its distal end to fuse with the protocone. The resultant hook-shaped structure ('crochet' of Stehlin, 1904*a*: 461) resembles that of P^4 of *P. cartailhaci* (Stehlin 1904*a*: pl. 12, fig. 1) and was the main reason for earlier misidentification of M26176 as *P. cartailhaci* (Hooker 1972). The 'crochet' also occurs in some individuals of *P. annectens* (Depéret 1917: pl. 9, fig. 2; Remy 1967: text-fig. 4). The cingulum is interrupted lingually.

Upper molars: In M26176, the protocone and paraconule are fused by wear on M^1 but not on the less worn M^{2} ^{3}. On the even less worn M26238, the paraconule is connected to the protocone. The paraconule protrudes less distally from the protoloph than in higher-crowned species like *P. annectens*. The buccal cingulum in M26176 is very weak (where this region is not eroded away), but it is not certain whether or not this constitutes individual variation; M26238 is also eroded here.

On the M^3s of both individuals (Pl. 24, figs 1b–c, 2a–b), the subterminal metastyle is absent from the basal half of the buccal wall, but a detached, more distal basal swelling could also be construed as part of the metastyle. In M26176, the hypostylar or distal cingular region is relatively expanded in length and height. It is formed from two curved crests, from the distal

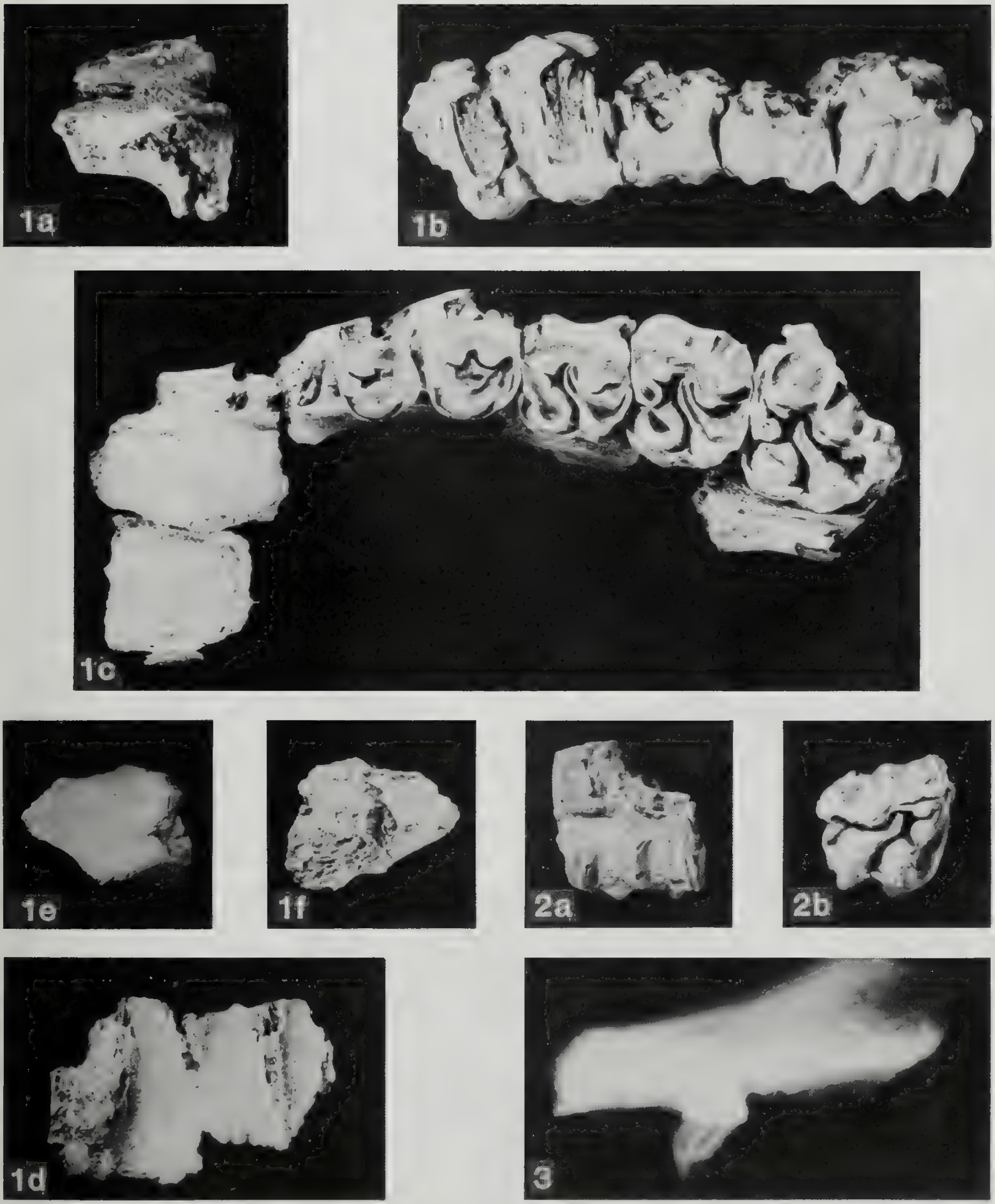
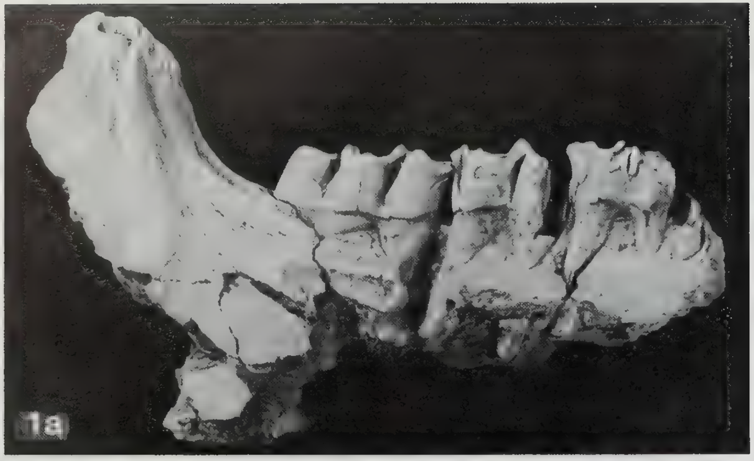
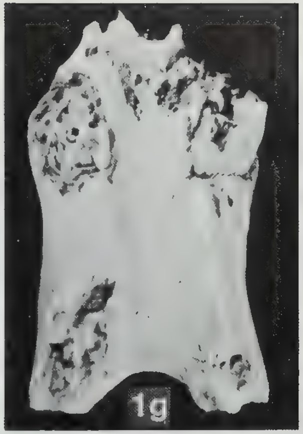


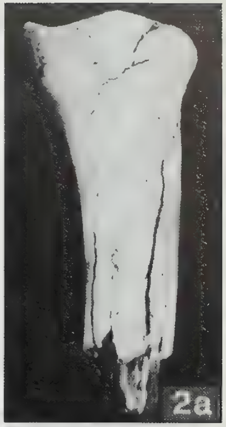
Plate 24 Light macrographs and x-ray of upper teeth and cranial fragments of *Plagiolophus*, × 1.

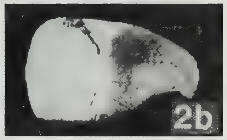
Figs 1–2 *Plagiolophus curtisi curtisi* sp. & subsp. nov. from Barton. Fig. 1a–f, **holotype** (M26176): a, left dorsolateral view of palatal fragment; b, buccal view of left P^3–M^3; c, ventral view of palatal fragment and occlusal view of P^3–M^3; d, dorsal view of palatal fragment; e, dorsal view of left frontal fragment; f, ventral view of left frontal fragment. Fig. 2a, b, buccal (a) and occlusal (b) views of right M^3 (M26238). See p. 356.

Fig. 3 *Plagiolophus fraasi* Meyer from Caylux: side view x-ray of right maxillary–premaxillary fragment with canine (M1673).


1a


1g


2a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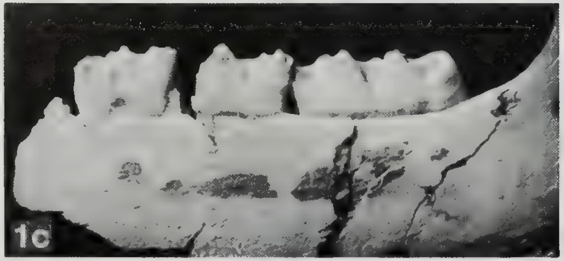
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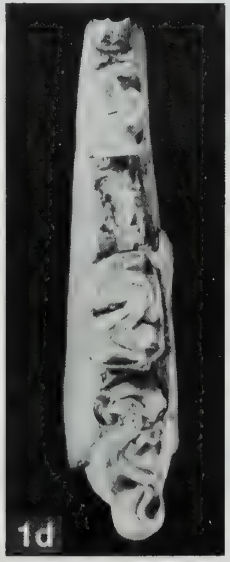
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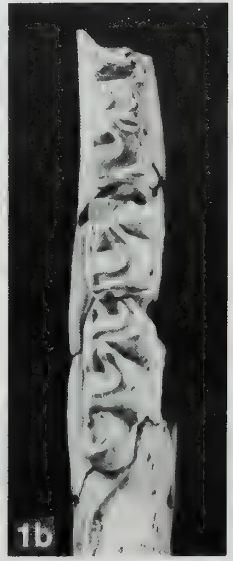
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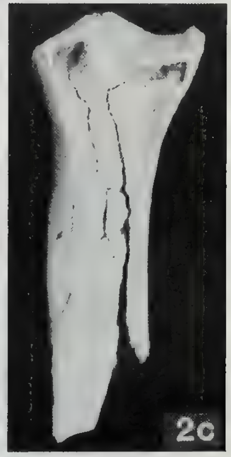
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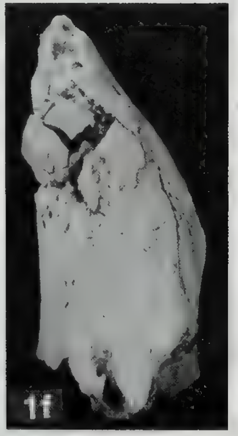
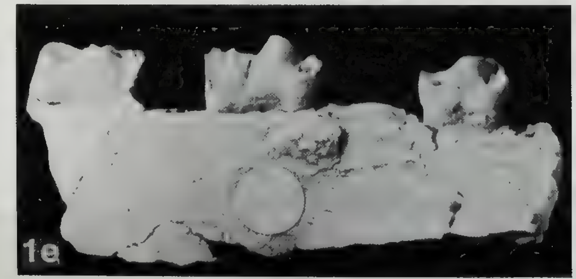

1f


1e

ends of the ectoloph and hypocone, which meet in the middle of the distal tooth margin; the ectolophal part projects distally more than the hypoconal part. M26238 is slightly less expanded distally than M26176, especially from the ectoloph, the distal hypoconal crest is lower and the two crests meet at a V-shaped distal concavity. Potential variation in this subspecies can only be observed on these two M^3s, and appears to be restricted to height of connection of paraconule to protocone (probably affecting the other molars as well) and degree of distal expansion. The curious subterminal metastyle is likely to be at least of common occurrence, if not a constant character. Too few specimens are known to test constancy of size but both M^3s are very close and the other teeth of M26176 are all larger than any of their equivalents (mainly different individuals) from Creechbarrow.

Lower premolars: The only remnant of P_3, the distal root, is as broad as on the Creechbarrow P_3s where a hypoconid is present (Pl. 25, fig. 1d). The P_3 of *P. annectens*, which lacks a hypoconid, has a small peg-like distal root. Moreover, the presence of a P_3 hypoconid in M26176 can be extrapolated from the presence of a P^3 metacone. P_4 is as far as can be observed typical for the genus.

Lower molars: Right M_1 is missing the mesial half of its lingual margin and is buccally eroded; both M_2s are better preserved and similar to M_1; right M_3 is complete. The metaconid and entoconid (and hypoconulid in M_3) have broad bases as seen lingually and tend to reduce the depth of the valleys enclosed by the first and second (and third on M_3) crescents (Pl. 25, fig. 1c, e). The effect is to give the teeth a robust appearance. Some specimens of other species of the genus have slight development of this feature, but its occurrence also in the Creechbarrow lower molars suggests that it might represent more than just individual variation in this case.

Skull: What remain of the side walls of the maxillae diverge dorsolaterally from the diastematal ridges more than in other species of the genus, presumably to house the large parallel upper canine roots. Only the left postcanine diastema is complete posteriorly and neither is complete anteriorly. The maximum measurable length is 14·4 mm, but they are estimated to have been at least 23·0 mm long, thus similar in relative length to those of *P. annectens*. The internal nares extend anteriorly to between the level of M^2 and M^3.

The infraorbital foramen is above the junction of P^3 and P^4, in contrast to *P. annectens* and *P. minor* where it is above the middle of P^4, and to *P. cartailhaci* and *P. fraasi* where it is above the anterior half of M^1. It migrates posteriorly in ontogeny, but moves little (less than the length of P^4) after the permanent premolars have erupted, a stage passed by the specimens considered here.

Immediately behind the infraorbital foramen there is part of a preorbital fossa (Pl. 24, fig. 1b). These may be of two kinds in the other equoid family, the Equidae (Gregory 1920): an upper ('lacrymal') and a lower ('malar'), which sometimes merge to form one. Its preserved anteroventral edge is sharp and extends posteriorly for the length of P^4 in the 'malar' region, but its dorsal extent is unknown. Gregory (1920: 282) stated that neither *Palaeotherium* nor *Paloplotherium* (= *Plagiolophus*) shows pronounced preorbital fossae, but, in addition to M26176, a maxilla of *P. fraasi* (M14734) from the Bembridge Marls of Bembridge shows part of a 'malar' fossa (Text-fig. 47B). Shallow preorbital depressions in *P. annectens* (Owen 1848*a*: pl. 3, fig. 1) and another *P. fraasi* specimen (M1733) from the Phosphorites du Quercy reach dorsally to the nasals, covering both 'malar' and 'lacrymal' regions, but like modern *Equus* lack sharp rims

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Plate 25 Light macrographs of lower teeth, jaw fragments and radius of *Plagiolophus*, × 1.

Fig. 1a–g *Plagiolophus curtisi curtisi* sp. & subsp. nov. from Barton, **holotype** (M26176): left mandibular ramus with P_4, M_{2-3} in occlusal (d) and lingual (e) views; right mandibular ramus with M_{1-3} in buccal (a), occlusal (b) and lingual (c) views; mandibular symphysis in right lateral (f) and dorsal (g) views. See p. 356.

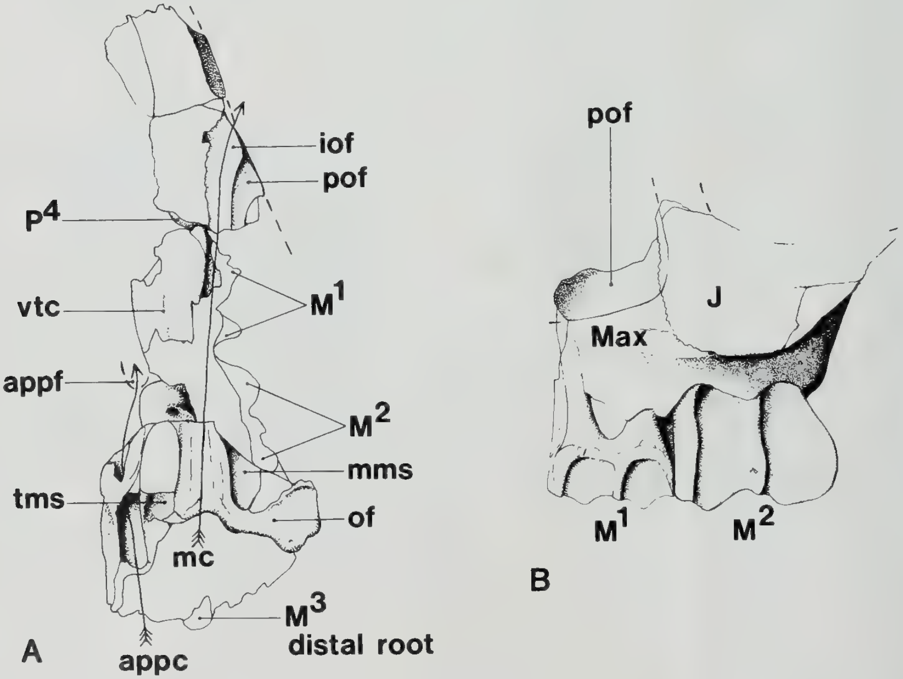
Fig. 2a–c ?*Plagiolophus* sp. indet. Proximal half of right radius from Barton (M34864). Views are anterior (a), proximal (b) and posterior (c). See p. 364.

(Gregory 1920: pl. 18). The apparent individual nature of this fossa in *Plagiolophus* contrasts with the hipparionine equids, where it is considered a generic character (Woodburne & Bernor 1980).

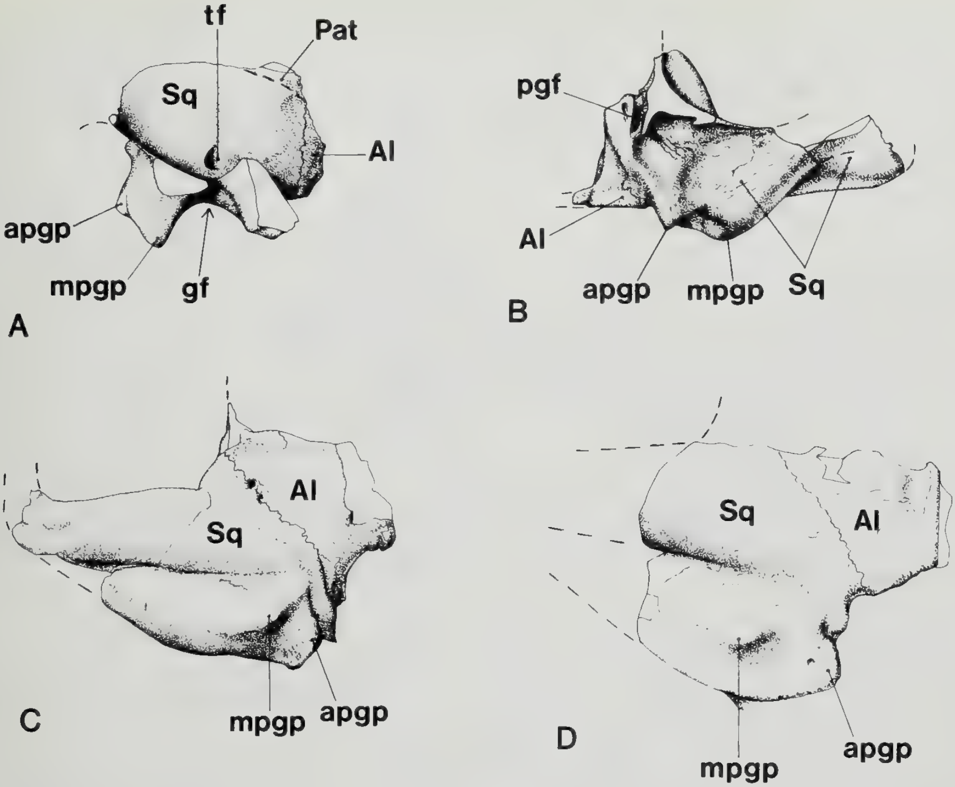
The cranial roof is known only from a fragment interpreted as part of the left frontal (Pl. 24, figs 1e–f; Text-fig. 49B). Its dorsal surface was flat, the supraorbital rim thin and the postorbital process thin and horizontal, in contrast to other species where it is gently domed with the supraorbital rims thick and the postorbital processes strongly downturned (e.g. Text-fig. 49A).

The leading edge of the orbit appears to have extended forward to a point above the junction of M^1 and M^2, further forward than in other species: M^2 midpoint in *P. annectens* and *P. fraasi* and M^{2-3} junction in *P. cartailhaci*. As for the infraorbital foramen, the orbital position is ontogenetically variable, but the specimens concerned have similarly worn teeth. The orbital floor and adjacent areas are incomplete but show the course of foramina and other structures (Text-fig. 47A). The orbital opening of the maxillary foramen and probably also the anterior postpalatine canal are as in *Pachynolophus lavocati* (Remy 1972: 60–62, text-fig. 9), *P. livinierensis* and *Hyracotherium leporinum* (Savage *et al.* 1965: 44, 46–47, text-fig. 20), *P. annectens* and *P. fraasi*.

The squamosal is perforated by a temporal canal, opening posteriorly at the postglenoid foramen and anteriorly at the temporal foramen (Text-fig. 48). The glenoid region differs from that of *P. fraasi* as follows: the main postglenoid process is slightly more prominent but less posteriorly expanded; and the smaller posteromedial accessory process is shorter but more sharply differentiated from the main process. Individual variation in these features is unknown.



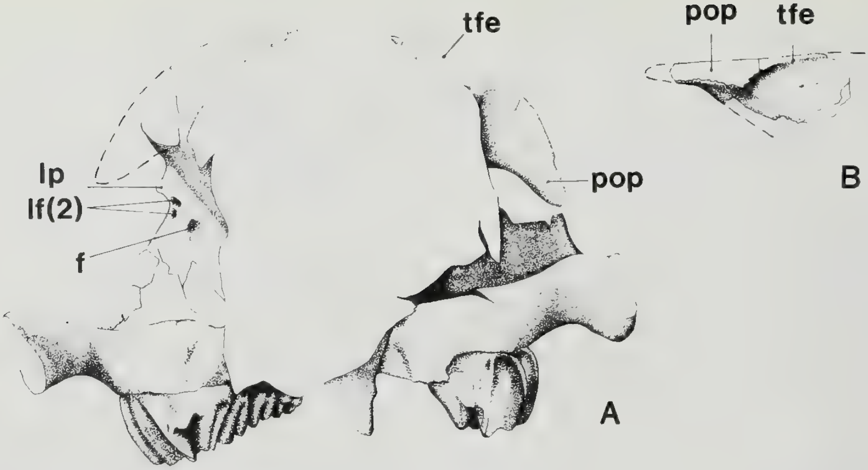
Text-figure 47 A, *Plagiolophus curtisi curtisi* sp. & subsp. nov., **holotype** M26176 from Barton Cliff. Dorsal view of maxillary fragment (incorporating part of the palatine) drawn as from the right side, consisting of the left maxillary fragment from P^4 forwards (reversed) and right maxillary fragment from M^1 backwards. Abbreviations: appc = anterior postpalatine canal; mms = maxillary sinus (main part), tms = maxillary sinus (turbinate part); vtc = ventral turbinate crest; for other abbreviations see Text-fig. 51, p. 366. × 1. B, *Plagiolophus fraasi* Meyer, M14734 from the Bembridge Marls of Bembridge. Lateral view of right maxillary fragment (reversed). × 1.



Text-figure 48 *Plagiolophus*, glenoid region. A–C, **holotype** of *Plagiolophus curtisi curtisi* sp. & subsp. nov. (M26176) from Barton Cliff. D, *P. fraasi* Meyer (M1733) from the Phosphorites du Quercy. A, lateral view of right glenoid region; B, posterior view of right glenoid region; C, ventral view shown as right glenoid region, but composite of right and left; D, ventral view of left glenoid region (reversed). Abbreviations: Al = alisphenoid; apgp = accessory postglenoid process; gf = glenoid fossa; mpgp = main postglenoid process; Pat = parietal; pgf = postglenoid foramen; Sq = squamosal; tf = temporal foramen. All × 1.

The mandibular symphysis is massive for housing the canine roots. Its ventral edge is angled anterodorsally below a point just behind the emergence of the canines. In contrast the small symphyses of other species have an even, anterior tapering, shape. The symphysis in M26176 terminates an unknown distance in front of the premolar row; in *P. annectens* it is just in front of P_2. The maximum length measurable on the lower diastemata of M26176 is 23·0 mm, the same as that estimated for the complete upper diastema. As there was apparently no tooth immediately following the breakage of the lower diastema, P_1 was probably absent, P_2 beginning the row behind the main mental foramen. In dorsal view the symphysis is only slightly concave laterally and the diastematal ridges are almost straight. In other species it is laterally more deeply concave and so are the ridges. Like the palate, the interdiastematal symphysial concavity is shallower in *P. curtisi* than in other species of *Plagiolophus*.

The anteromedial edge of the ascending ramus forms an acutely angled ridge because the masseteric ridge lies posterolateral to it. This contrasts with other species where both ridges normally lie side by side and are weaker and more rounded. The curvature of the posterior edge of the coronoid process indicates a more gentle slope towards the condyle than in other species. The same character in a specimen of *Paraplagiolophus codiciensis* (MNHN, labelled 'M. Guérin Cat. 20') is associated with a more posteriorly expanded angular region and a lower, less recurved coronoid process. The condyle is similar to that of *P. annectens* but is thicker and



Text-figure 49 *Plagiolophus*, posterior cranial views. A, syntype of *P. annectens* (Owen) (29729) from Hordle Cliff. B, **holotype** of *P. curtisi curtisi* sp. & subsp. nov. (M26176) from Barton Cliff. Abbreviations: f = fossa; lf = lacrymal foramina; lp = lacrymal process; pop = postorbital process; tfe = edge of temporal fossa. × 1.

has a sharp anterolateral ridge. Posteroventrally the beginning of the angular edge is orientated more like *P. codiciensis* than a species of *Plagiolophus* (Text-fig. 50).

Tentatively referred radius: The proximal articulation measures 14·0 mm anteroposteriorly and 23·3 mm mediolaterally. Both are probably slight underestimates as the bone is somewhat eroded anteriorly and laterally. The maximum length of the incomplete shaft is 56·5 mm (Pl. 25, fig. 2). It is very similar in size and morphology to radii of *P. annectens* from Hordle Cliff and La Débruge and in morphology to those of *P. minor* from La Débruge. All species of *Palaeotherium* examined in comparison had a medially bowed radius, resulting in the proximal articulation being slightly oblique, compared to the nearly straight *P. annectens* radius. *Palaeotherium* radii also tend to be shorter and broader but this feature cannot be observed on M34864.

Plagiolophus curtisi creechensis subsp. nov.
(Pl. 26, fig. 1; Text-figs 45, 46, 52C–D, 53; Table 28)

v. *1977b* *Plagiolophus* aff. sp. nov.; Hooker: 141.
v. *1980* *Plagiolophus* sp. 1; Hooker & Insole: 42.

NAME. From the tithing of Creech in the parish of Church Knowle, overlooked by Creechbarrow.

HOLOTYPE. Associated upper and lower dentitions (M36181): left C^1, P^2–M^3; right P^2–M^3; left I_2?, C_1, P_2–M_3; right C_1, P_4–M_3. Numerous indeterminate fragments, probably mainly from the jaws, are likely also to be associated.

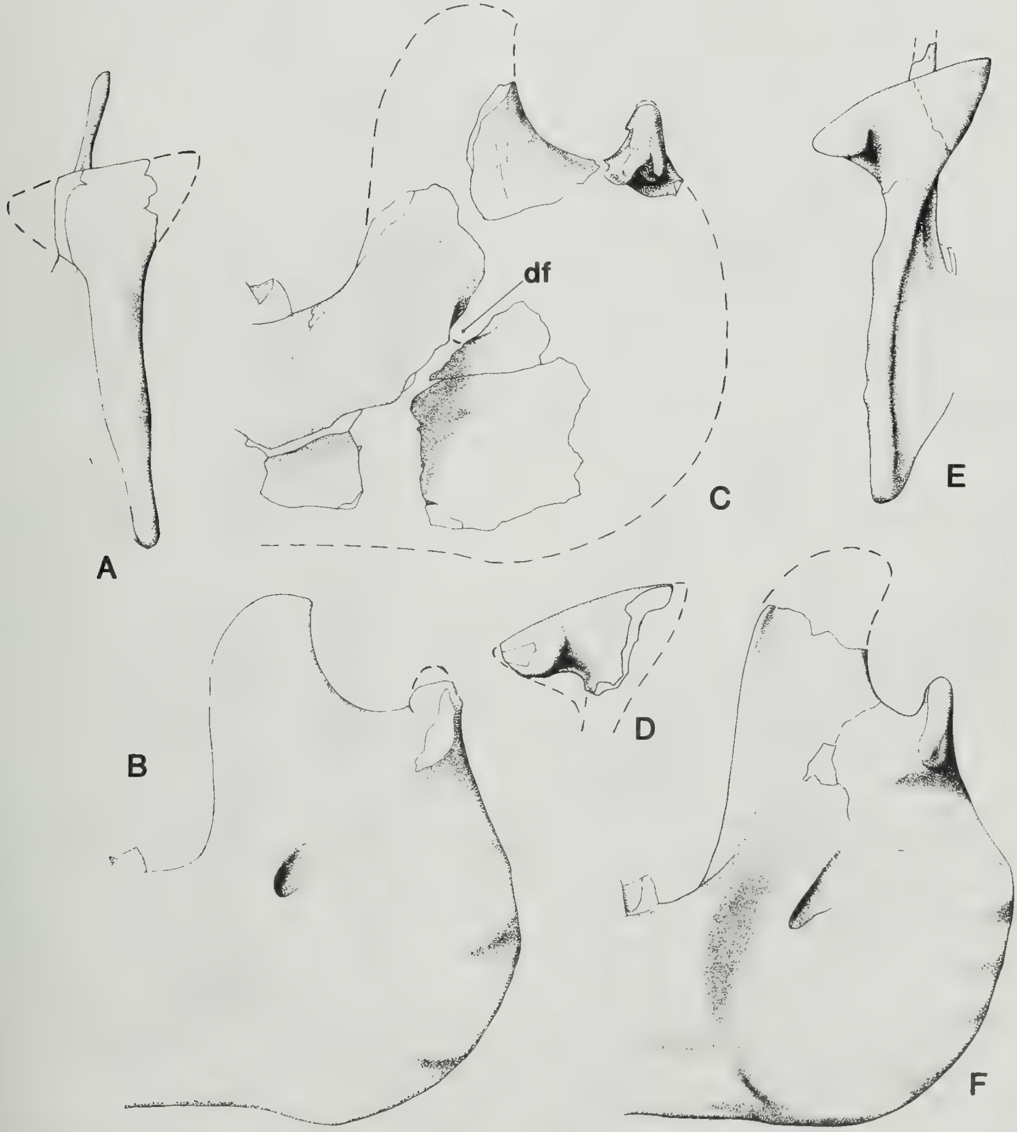
PARATYPES. (18): Upper canine (M37473); two P^2s (M37474–5); two or three P^3s (M37476–7, ?M37478); P^4 (M37479); four fragmentary upper molars, mainly if not all $M^{1/2}$s (M37480–3); two P_2s (M36182, M37484); P_3 (M37485); two $M_{1/2}$s (M37486–7); M_3 (M37709); lower molar trigonid fragment (M37488).

DOUBTFULLY REFERRED MATERIAL. Two incisors (M37489–90); left petrosal (M37491).

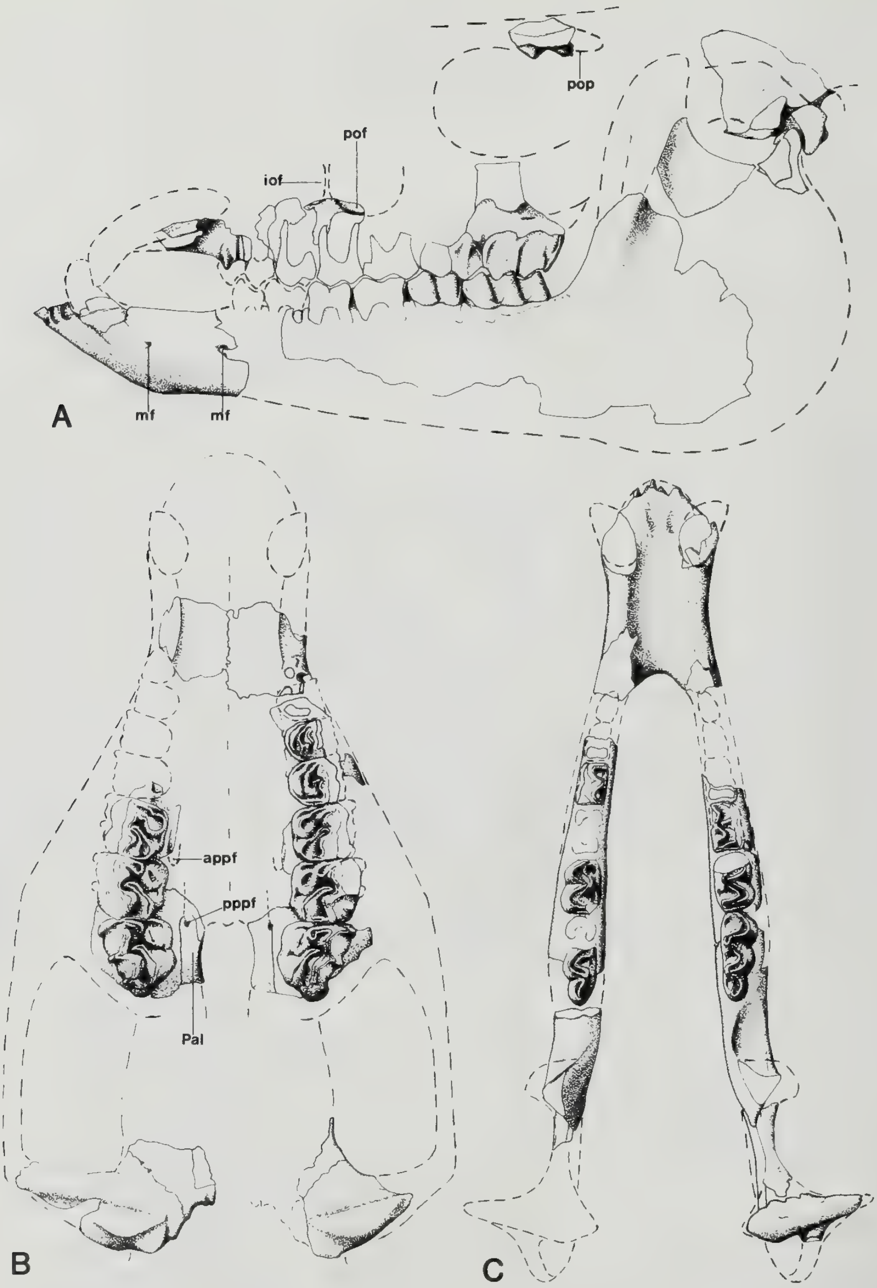
HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. 1, small (M^2 length 13·0 mm); 2, P^{3-4} protocones conical; 3, small metaconule on upper molar metaloph; 4, no accessory subterminal metastyle.

DESCRIPTION. *Canines*: It has been shown above that the canines of M26176 are not splayed like those of other species of *Plagiolophus* but have essentially parallel orientation and the uppers are more laterally spaced than the lowers. Because of ectental cheek tooth motion in *Plagiolophus*, the striations produced on the transverse-vertical facets of the canines in the 'splayed' species run longitudinally on the uppers and transversely on the lowers (Text-fig.



Text-figure 50 Ascending mandibular rami (shown as right) of *Plagiolophus* and *Paraplagiolophus*, ×0·75. A–B, *Paraplagiolophus codiciensis* (Gaudry) (MNHN unnumbered) from Jumencourt (Upper Calcaire Grossier); posterior and medial views respectively of left ascending ramus (reversed). C D, *Plagiolophus curtisi curtisi* sp. & subsp. nov., **holotype** (M26176) from Barton Cliff; medial and posterior (condyle only) views respectively of fragmentary right ascending ramus. E–F, *Plagiolophus annectens* (Owen) (28229, Bravard Cat. no. G148) from La Débruge; posterior and medial views respectively of left ascending ramus (reversed). Abbreviation: df = dental foramen.



Text-figure 51 *Plagiolophus curtisi curtisi* sp. & subsp. nov., holotype (M26176) from Barton Cliff. Partial reconstruction of skull, × 0·5. A, left lateral view of left and right composite. B, ventral view of cranium. C, dorsal view of mandible. Abbreviations: appf = anterior postpalatine foramen; iof = infraorbital foramen; mf = mental foramen; Pal = palatine; pof = preorbital fossa; pop = postorbital process; pppf = posterior postpalatine foramen.

52A–B). Observation of striations on *P. curtisi creechensis* should confirm whether or not the canine angle was as in *P. curtisi curtisi* or as in the other species. Unfortunately no striations are preserved, although parts of the facets remain on some of the incomplete canines. The apical half of the left lower canine of the holotype preserves almost all the facet, including part of its basal margin towards the lingual side. Here the facet margin slopes buccobasally, leaving a lingual ridge unworn at the same crown level. If wear had been completely transverse, this ridge would almost certainly have sustained wear (Text-fig. 52C–D). It is thus tentatively concluded that wear was oblique and that the canines in the lower jaw at least had approximately parallel orientation as in *P. curtisi curtisi.*

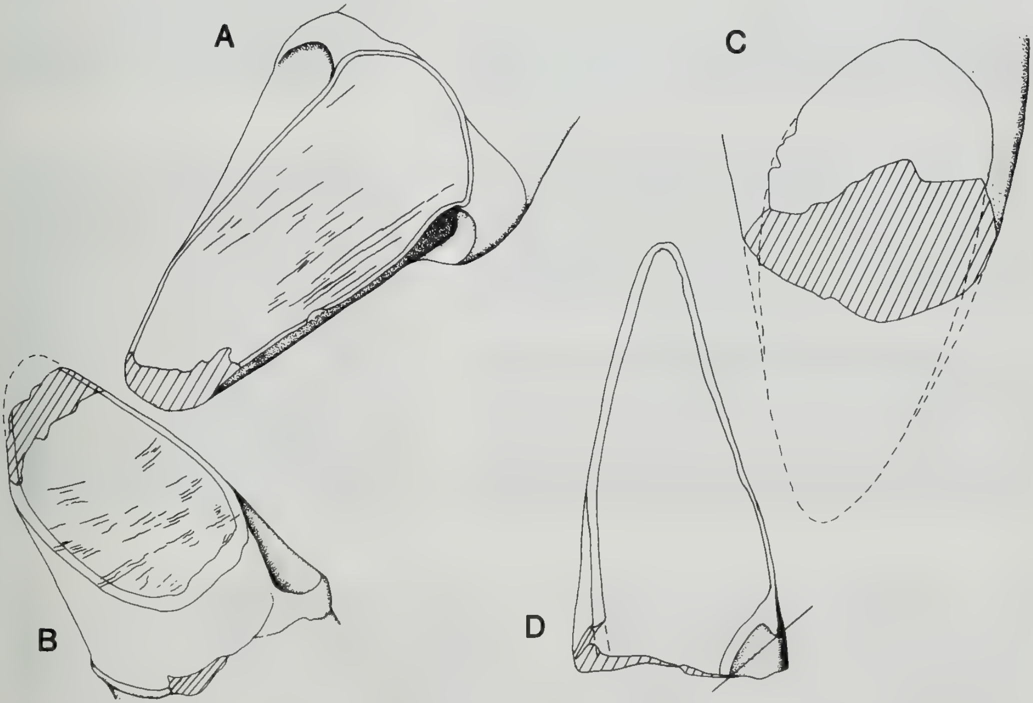
The lower canines are almost as large as those of M26176, whilst an upper (M37473) fits reasonably well in the remains of the upper alveoli of M26176.

Upper premolars: P^1 is known to have existed from mesial interstitial facets on the P^2s.

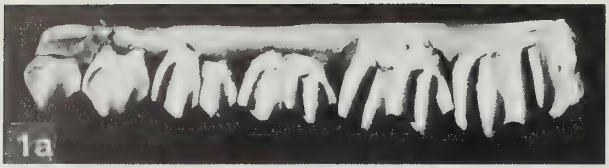
Complete P^2s from two individuals (M36181, M37474) show the metacone and mesostyle to be absent, but the paraconule to be a distinct cusp. On one the metaconule is joined to the distal cingulum, on the other it is isolated.

The only complete P^3 is the left one of the holotype. It has equal-sized paracone and metacone lying close together with the paracone bulging lingually more than the metacone, as in M26176. The large metaconule is linked by a narrow crest (missing on the right holotype P^3) to the distal cingulum. There is no mesostyle.

There are two individuals to show variation in P^4. At similar wear stages, M36181 shows the metaconule joined to the protocone in a complete 'crochet' structure as in M26176, whereas in



Text-figure 52 Occlusal views of canines in *Plagiolophus* showing orientations at beginning of buccal phase. A–B, *P. fraasi* Meyer from the Phosphorites du Quercy; C–D, *P. curtisi creechensis* subsp. nov. from Creechbarrow. A, Right upper canine (M1673); B, left lower canine (M1750); C, ?left upper canine (reversed) (M37473); D, left lower canine. Wear facets of A and B show striations indicating direction of motion; oblique line delimiting lower edge of facet in D indicates suggested maximum transverse angle of mastication. Oblique hatching indicates broken surfaces. × 5.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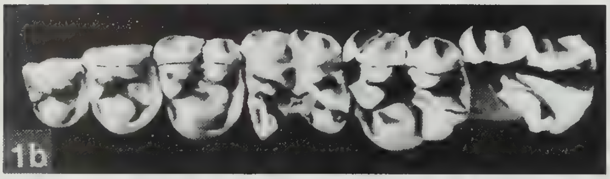
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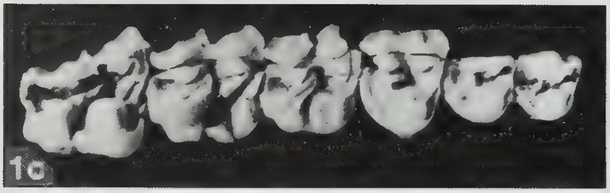
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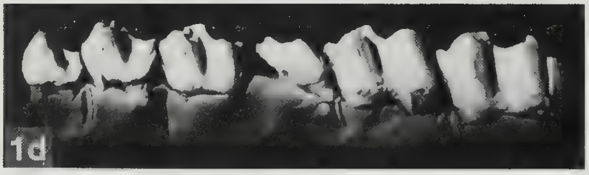
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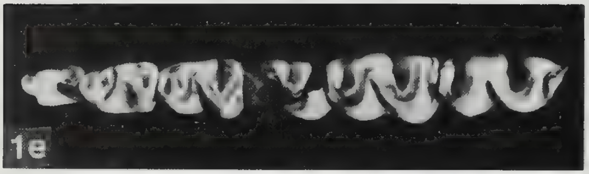
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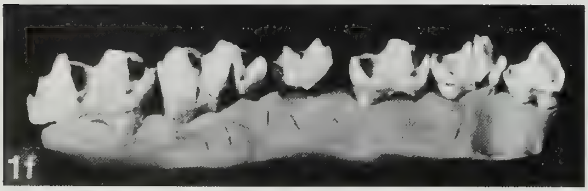
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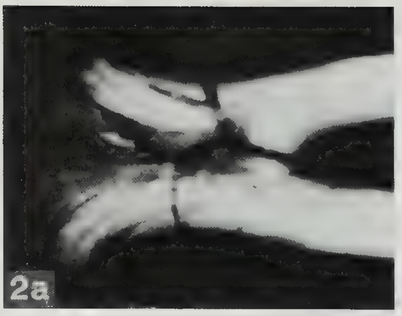
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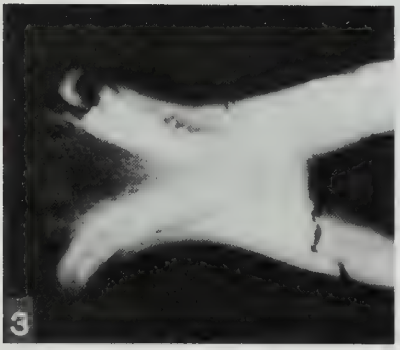
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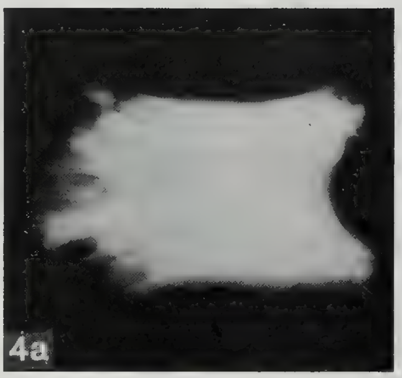
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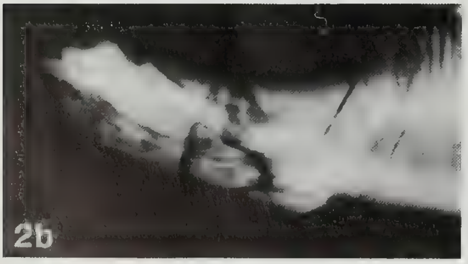
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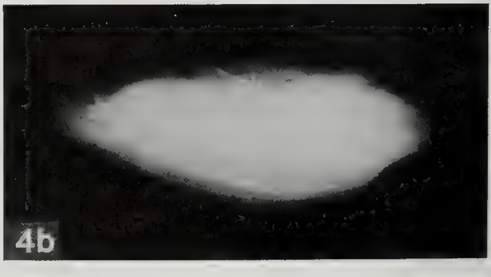
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M37479 the distal end is bent lingually at right angles, separated from the protocone, and a small bulge crosses the valley almost meeting the distal cingulum. The mesial end of the metaloph is simple in both specimens. M36181 is the only individual complete enough to show that, although a mesostyle is absent, a very faint ridge is present at the base and top of the ectoloph between the paracone and metacone.

The cingulum is interrupted lingually on P^{2-4}, but the contrast with *P. curtisi curtisi* is likely to be of an individual nature.

Upper molars: Only the holotype shows distinguishing characters. The buccal cingulum is interrupted opposite the metacone on M^3, otherwise it is complete although not very strong. Degree of separation of the paraconule from the protocone is very similar to M26176. The degree of distal expansion of M^3 is intermediate between that described above for M26176 and M26238, but similar to both in style. The subterminal metastyle is absent from this tooth in M36181, but the more distal basal swelling is present.

Lower premolars: Available P_2s have no mesial interstitial facet, so it is concluded that P_1 was absent.

In three P_2s there is slight variation in the size of the metaconid. It ranges from insignificant and style-like to three-quarters the height of the protoconid. There is a low, almost longitudinal metalophid which has a slight lingual bend at its distal end, the only recognizeable homologue of the hypoconid. The buccal cingulum varies from weak and interrupted to completely missing.

The hypoconid is smaller on P_3 (M36181) than on P_4 and the whole talonid is much lower and narrower than the trigonid. The small size of the talonid corresponds to the proximity of the paracone and metacone of P^3 with which it occludes. Because of disto-occlusal flaring, the hypolophid of M37485 has been almost entirely removed by heavy wear.

On the holotype left P_4 the talonid is slightly wider than, and nearly as high as, the trigonid. The latter is less open than on P_3, being more like that of the molars but with a weaker paralophid.

Lower molars: The shallowing of the valleys already mentioned under *P. curtisi curtisi* is hardly visible on M36181, but it is present in a curious form on an M_3 (M37709) which has the hypoconulid and part of the hypolophid broken away. Lying in the valley enclosed by the second crescent there is a transverse rib which merges lingually with a mesial extension of the base of the entoconid. Apart from slightly lower crown height, the lower molars are otherwise similar to those of *P. annectens*.

Tentatively referred petrosal: The identification of this isolated bone with *P. curtisi creechensis* should be considered as no more than very tentative. The only perissodactyl genus in the Creechbarrow fauna the right size is *Plagiolophus*, but as so few published accounts of the ear region of European perissodactyls exist, the taxonomic relevance of morphological differences cannot easily be assessed.

M37491 has been compared with an as yet undescribed petrosal *in situ* in a cranium of *P. fraasi* (M1733) from the Phosphorites du Quercy, two isolated petrosals from the Hordle Cliff

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Plate 26 Light macrographs of cheek teeth and x-rays of symphyses of *Plagiolophus*, × 1.

Fig. 1a–f *Plagiolophus curtisi creechensis* sp. & subsp. nov., **holotype** (M36181) from Creechbarrow. a, buccal view of left P^2–M^3; b, occlusal view of left P^2–M^3; c, occlusal view of right P^2–M^3; d, buccal view of left P_2–M_3; e, occlusal view of left P_2–M_3; f, lingual view of left P_2–M_3; note that hypoconulid lobe is broken on M_3. See p. 364.

Figs 2–3 *Plagiolophus annectens* (Owen) from Hordle Cliff. X-rays of mandibular symphyses. Fig. 2a, b, younger individual (BM(NH) 29730) in dorsal (a) and lateral (b) views. Fig. 3, older individual (BM(NH) 29705) in dorsal view.

Fig. 4a, b *Plagiolophus curtisi curtisi* sp. & subsp. nov., **holotype** from Barton Cliff (M26176). X-ray of mandibular symphysis in (a) dorsal and (b) lateral views. See p. 356.

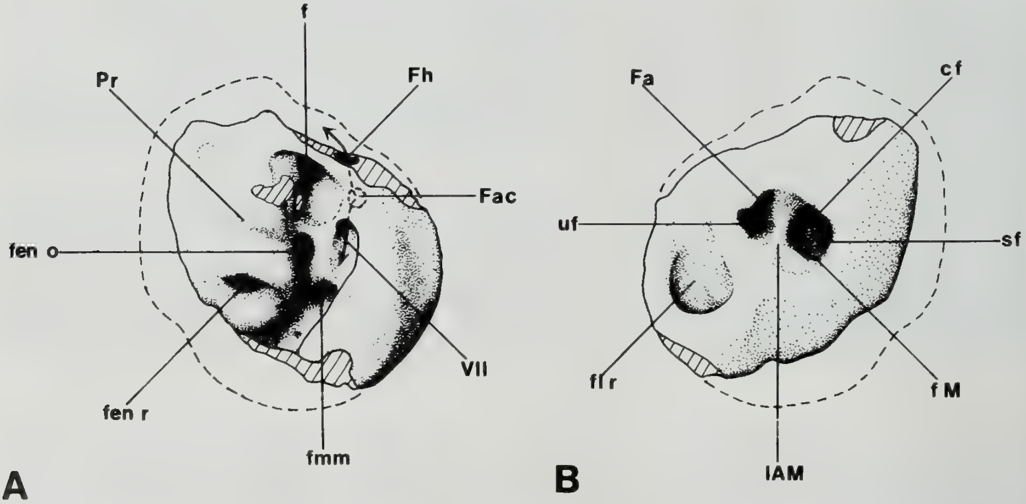
Mammal Bed (R. Gardner private collection) and figures and descriptions of *Pachynolophus livinierensis* Savage, Russell & Louis 1965 (Savage *et al.* 1965: 48, 51–52, text-fig. 22; pl. 1) and *Pachynolophus lavocati* Remy 1972 (Remy 1972: 66–69, text-fig. 11; pl. 4). (Note that Savage *et al.* 1965: pl. 1 shows a right petrosal, not a left as stated).

The specimen is worn and broken but its significant differences from the other petrosals mentioned above will be described. Terminology used here follows Savage *et al.* (1965), MacIntyre (1972) and Remy (1972). Most of the edges of the bone are broken away except for the posterior half of the lateral edge. The main position of the foramina and other structures are indicated in Text-fig. 53.

In ventral view, the basic pattern of the foramina is the same in all the material mentioned but, in contrast to the others, in M37491 there is a facial canal bridge. The Fallopian hiatus is thus more anterior and occurs in an area of marginal breakage. The rim of the fenestra ovalis is also raised and, anteromedially of these two areas, there is left a distinct oval fossa in the area of the sulcus arteriosus promontorii.

On the dorsal surface, the two depressions of the internal auditory meatus have an anterolateral/posteromedial spatial relationship as in M1733. The Fallopian aqueduct is overhung by an anterior lip and is orientated anterodorsally. The utricular fossette occupies all the posterolateral half of the anterolateral depression. The cochlear fossette is large and the saccular fossette posterolateral to it. The foramen of Morgagni is very small and sharp-rimmed and almost vertically perforates the posterolateral wall of the posteromedial depression. Lateral to the internal auditory meatus is the floccular (subarcuate) fossa, which in M1733 and the Hordle Cliff specimens is absent.

Discussion of *P. curtisi.* Characters 6, 7 and 8 of the diagnosis of *P. curtisi* are shared with *P. annectens*, *P. minor* and *P. fraasi* of the Ludian. Characters 3, 4, 5, 12, 17, 18, 19 and 20 are shared with an undescribed species from the late Lutetian of Egerkingen γ. Characters 10, 11 and 15 are intermediate between the two types; so are the proximity of the P^3 paracone and



Text-figure 53 Eroded left petrosal (M37491) from Creechbarrow, possibly belonging to *Plagiolophus curtisi creechensis* subsp. nov. A, ventral view; B, dorsal view. Abbreviations: cf = cochlear fossette; f = unnamed fossa; Fa = Fallopian aqueduct; Fac = Fallopian aqueduct (concealed by facial canal bridge); fen o = fenestra ovalis; fen r = fenestra rotunda; Fh = Fallopian hiatus; flr = floccular recess (subarcuate fossa); fM = foramen of Morgagni; fmm = fossa muscularis minor; IAM = internal auditory meatus; Pr = promontorium; sf = saccular fossette; uf = utricular fossette; VII = facial canal (probable course of VIIth (facial) nerve). Oblique hatching indicates broken surfaces. × 3·3.

metacone and small size of the P_3 hypoconid. Characters 9 and 16 are unique to *P. curtisi*. The characters of the earlier species are considered primitive and those shared by the later species advanced. The intermediate characters fit well with the known Bartonian age of the nominate subspecies, whilst its unique characters suggest that it did not give rise to any other known species.

The presence of P^3 metacone and P_3 hypoconid in this and the undescribed Egerkingen γ species has relevance to an understanding of the affinities of *Plagiolophus*. It supports the derivation of this genus from a low-crowned palaeothere such as *Propalaeotherium* (referred to Equidae by Savage *et al.*, 1965) by increase in crown height. The non-molariform $P\frac{3}{3}$ in advanced *Plagiolophus* can then be regarded as a secondary simplification, rather than as evidence of derivation from a condylarth stock independent of *Hyracotherium* (see Butler, 1952*a*, 1952*b*; Remy, 1967, 1976). Detailed discussion of this question will be covered elsewhere.

When first studying the Creechbarrow and Barton *Plagiolophus* material, three alternative classifications appeared possible: 1, simply to consider all the material as one taxonomic unit at species level, on the basis of the unique characters listed above; 2, to separate the two assemblages as different species on the basis of a few minor characters; or 3, to describe them as one species but giving each assemblage a different subspecific name. The mixing of the assemblages resulting from solution 1 was abandoned as confusing. The small size of the assemblages does not give a clear enough idea of the constancy or variation of the distinguishing characters, so solution 2 was abandoned. The apparently constant size difference between the two assemblages is only slightly less than that which occurs between two closely related sympatric species (*P. annectens* and *P. minor* from La Débruge), so solution 3 was used.

Because both subspecies occur in the same general area (Creechbarrow and Barton are only 32 km apart) and because they have not been found in continental European Bartonian sites (where nevertheless other species of *Plagiolophus* are known), it is logical to consider them as probably stratigraphical subspecies or stages in a single lineage. Of the characters which distinguish the two subspecies, 2 and 3 can be considered primitive in *P. curtisi creechensis* and advanced in *P. curtisi curtisi*, as they are shared with *P.* sp. from Egerkingen γ and *P. annectens* respectively. Character 4 may also be an advanced character for *P. curtisi curtisi*, but it occurs in Auversian *P. cartieri* and not in any of the other species, older or younger. The evidence as a whole suggests a slightly earlier age for the Creechbarrow Limestone than for Barton Clay beds D/E.

Genus ***PALAEOTHERIUM*** Cuvier 1804

TYPE SPECIES. *P. magnum* Cuvier 1804. Première Masse du Gypse, Montmartre, Paris, France.

INCLUDED SPECIES. *P. eocaenum* Gervais 1875, *P. siderolithicum* (Pictet & Humbert 1869) Franzen 1968, *P. lautricense* Stehlin 1904*a*, *P. ruetimeyeri* Stehlin 1904*b*, *P. pomeli* Franzen 1968, *P. castrense* Noulet 1863, *P. medium* Cuvier 1804, *P. crassum* Cuvier 1805, *P. renevieri* Stehlin 1904*b*, *P. muehlbergi* Stehlin 1904*b*, *P. curtum* Cuvier 1812, *P. duvalii* Pomel 1853, *P. crusafonti* Casanovas-Cladellas 1975.

RANGE. Late Lutetian–late Ludian, Europe. See Franzen (1968) for details of horizons and localities of the species.

DIAGNOSIS. See Franzen (1968: 16).

Palaeotherium aff. ?***muehlbergi*** Stehlin 1904*b*

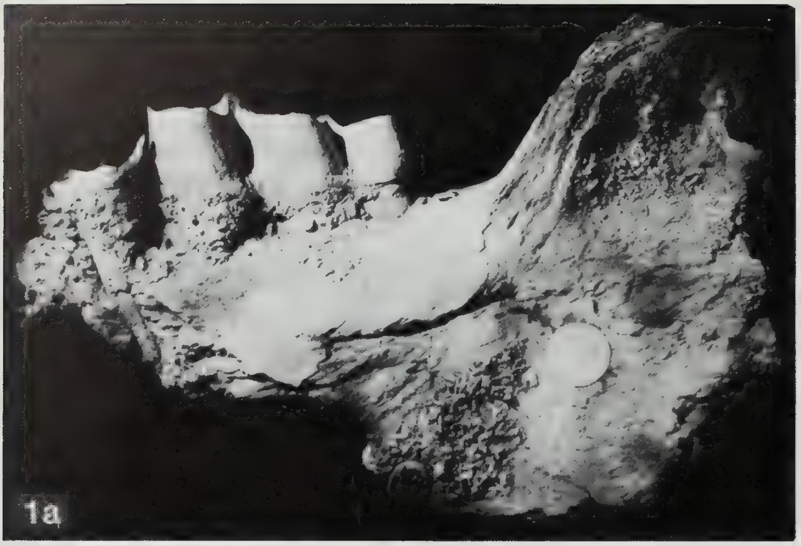
(Pl. 27, fig. 1)

vp. *1980* *Palaeotherium* sp.; Hooker & Insole: 43.

LECTOTYPE of *P. muehlbergi*. Left P^{2-3} (Paläontologisches Institut und Museum Zürich no. A/V 242). Ludian fissure filling, Obergösgen, Switzerland.

RANGE of *P. muehlbergi*. Ludian; England, France, Switzerland and West Germany.

DIAGNOSIS of *P. muehlbergi*. See Franzen (1968: 102, 104).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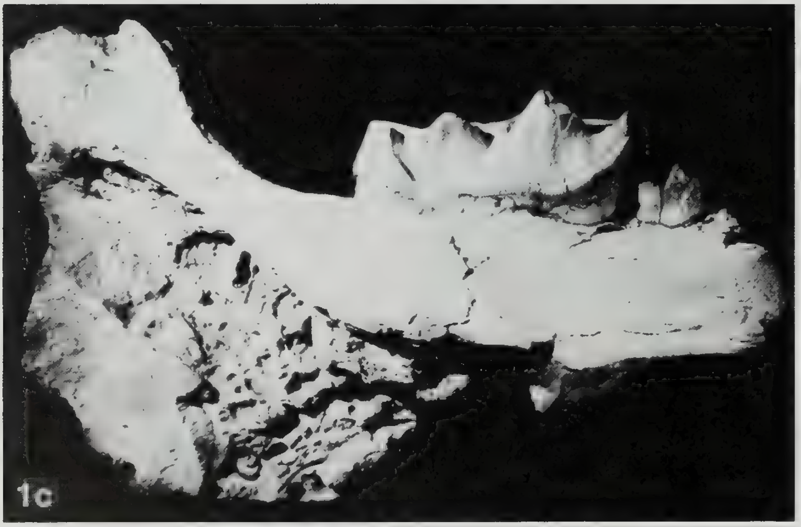
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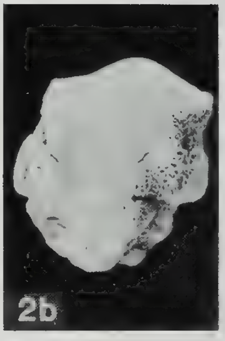
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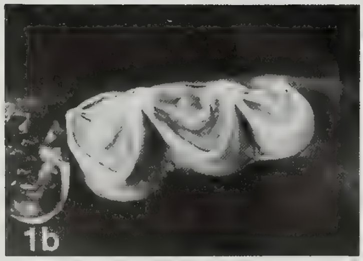
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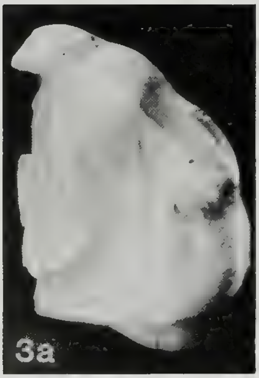
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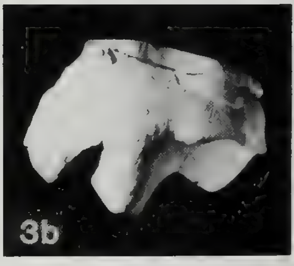
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MATERIAL. Left mandibular fragment with distal fragment of M_2 and complete M_3 (M34865).

HORIZON AND LOCALITY. Barton Clay Formation (not *in situ*), on high terrace of Barton Cliff below Naish Estate, near Barton-on-Sea, Hampshire; probably about SZ 223931. The jaw cavity is filled with brown concretionary claystone full of moulds of molluscs, mainly *Turritella*; there is no glauconite. The preservation thus suggests Bed F, which was exposed here at the time of collection in 1976 by Mr I.C. Daniels of Southbourne, Dorset.

DESCRIPTION. The distal width of the remains of M_2 is 16·4 mm. The M_3 is 35·9 mm long; the trigonid width is 15·9 mm, the talonid width is 13·9 mm and the hypoconulid width 10·6 mm.

The M_3 is moderately worn and exact crown height is unknown, but comparison with specimens at similar wear stages indicates that it is fairly low crowned for *Palaeotherium*.

The crescents of M_3 are sharply convex, not blunt and rounded as in *P. magnum*. The hypoconulid lobe is moderately bent and the distal limb is orientated essentially lingually. The extent of wear on the hypoconulid and hypoconid suggests that when unworn the former was not much lower than the latter.

The lingual cingulum is mainly strong but fades between the entoconid and hypoconulid. The buccal cingulum is weak and interrupted at the protoconid, hypoconid and hypoconulid.

COMPARISONS AND DISCUSSION. Eight described species can approach the dimensions of the Barton specimen: *P. pomeli* (Marinesian), *P. ruetimeyeri*, *P. castrense* (late Lutetian–Marinesian), *P. medium*, *P. crassum*, *P. curtum*, *P. renevieri* and *P. muehlbergi* (Ludian).

P. pomeli differs in having higher-crowned teeth and an M1–3 enlargement.

P. medium and *P. crassum* have relatively longer and narrower M_3s with a more continuous buccal cingulum. Moreover, the earlier subspecies, which are closer in age to the Barton specimen, are more different in size than the later ones. These species and *P. curtum* tend to have rounder, less angled crescents. *P. renevieri* is very similar to *P. crassum*.

The remaining three species are very similar to M34865. Both *P. ruetimeyeri* and *P. castrense* have strong continuous buccal cingula, but on *P. muehlbergi* these can be weak and interrupted. *P. muehlbergi* also has characteristically angled crescents but the hypoconulid has a stronger and more mesially directed distal hook.

Of the Marinesian species in the above list, the M_3 from Robiac, attributed to *P.* aff. *ruetimeyeri ruetimeyeri* by Franzen (1968: pl. 4, fig. 8), is closest in size, being only very slightly smaller. This too, though, has a continuous buccal cingulum.

Franzen (1968: 109) considered the possibility that *P. muehlbergi praecursum* Franzen 1968 (the earliest subspecies from Hordle Cliff) could have evolved from *P. ruetimeyeri*, but that the typical and best known assemblage from Egerkingen α was very much older and more primitive than *P. muehlbergi*. He noted that the Robiac specimens did not provide enough information to support this derivation. The Barton specimen demonstrates the presence in the Marinesian of a *P. muehlbergi*-like species, but more complete material would be necessary to test out the above evolutionary hypothesis and to provide a more accurate identification.

Palaeotherium sp. indet.

(Pl. 27, fig. 2)

v. *1979* cf. *Palaeotherium* sp.; Kemp *et al.*: 102.
vp. *1980* *Palaeotherium* sp.; Hooker & Insole: 43.

MATERIAL. Lateral fragment of distal articulation of left humerus (M36491).

Plate 27 Light macrographs of *Palaeotherium* and *Lophiodon*, × 1.

Fig. 1a–c *Palaeotherium* aff. ?*muehlbergi* Stehlin (M34865) from Barton Cliff. Left mandibular fragment with M_3 and distal root of M_2. a, buccal, b, occlusal and c, lingual views. See p. 371.

Fig. 2a, b *Palaeotherium* sp. indet. (M36491) from Elmore. Mediodistal fragment of right humerus. a, anterior and b, distal views. See p. 373.

Fig. 3a, b *Lophiodon* cf. *cuvieri* Filhol (GM.978110–3) from Elmore. Cast (M41977) of left M^3, not sprayed with ammonium chloride. a, occlusal and b, buccal views. See p. 374.

Horizon and locality. Elmore Member, Barton Clay Formation (not *in situ*), foreshore at Elmore, near Lee-on-Solent, Hampshire.

Description. No useful measurements can be taken of this fragment. It compares very well in size and morphology with the relevant part of a complete humerus of *P. magnum stehlini* Depéret 1917 (BM(NH) 29744a) from Hordle Cliff. The characters available, however, do not appear to be species characteristic. The only *Palaeotherium* species of the appropriate size known from the Auversian is *P. castrense*. Specific identification, however, cannot be made, although it seems unlikely that it was conspecific with the specimen from Barton. One must hope that this locality will eventually yield some dental remains of the genus.

Suborder **ANCYLOPODA** Cope 1889

(rank emend. Radinsky 1964) (*sensu* Hooker 1984)

Family **LOPHIODONTIDAE** Gill 1872

Type genus. *Lophiodon* Cuvier 1822.

Remarks. The classification by Radinsky (1964: 3–4, 7–9) and Savage *et al.* (1966: 31–35) of *Lophiaspis* Depéret 1910 and *Paleomoropus* Radinsky 1964 in the family Eomoropidae Matthew 1929*a* is followed here, rather than that by Fischer (1964: 62–64, 67, fig. 21; 1977*a*: 917–918), who included them in the Lophiodontidae.

Range. Same as *Lophiodon* (q.v.).

Genus ***LOPHIODON*** Cuvier 1822

Type species. *Palaeotherium tapiroides* Cuvier 1812. Middle Lutetian; Bouxwiller, Alsace, France.

Included species. *L. remensis* Lemoine 1878, *L. tapirotherium* Desmarest 1822, *L.? buchsowillanum* Desmarest 1822, *L. parisiense* Gervais 1852, *L. cuvieri* Filhol 1888*a*, *L. thomasi* Déperet 1906, *L.? isselense* Fischer 1829, *L. rhinocerodes* Rütimeyer 1862, *L. lautricense* Noulet 1851, *L. sardus* Bosco 1902, *L.? leptorhynchum* Filhol 1888*a*. For additional doubtful species see Fischer (1964: 67). For differing views of species, see Fischer (1964, 1977*a*, 1977*b*), Jaeger (1971) and Sudre (1971).

Discussion. Dedieu (1977, June) placed *L. buchsowillanum* (type species), *L. isselense*, *L. leptorhynchum* and *L. compactus* Astre 1960 (the last raised to species level) in his new genus *Paralophiodon*, which he referred to a new monotypic subfamily Paralophiodontinae of the family Isectolophidae. Fischer (1977*a*, July) placed *L. buchsowillanum* in his new monotypic lophiodontid genus *Rhinocerolophiodon* (thus a junior objective synonym of *Paralophiodon*) and referred *L. leptorhynchum* to *Lophiaspis*. Until more detailed evidence is published, a conservative approach is adopted here.

Range. Late Ypresian to Bartonian (Marinesian), Europe and possibly south-west Asia.

Diagnosis. See Fischer (1977*b*: 1129).

Lophiodon cf. ***cuvieri*** Filhol 1888*a*

(Pl. 27, fig. 3)

v. *1980* *Lophiodon* cf. *cuvieri* Filhol; Hooker & Insole: 43.

Syntypes of *L. cuvieri*. Cranium and left mandibular ramus. Upper Calcaire Grossier (late Lutetian); Jouy, Marne, France (Filhol 1888*a*: 144–154; pls 14–15; pl. 16, figs 3–5; pl. 17, fig. 5). Neither Schroeder (1916) nor Fischer (1964) were able to find the specimens although they were stated to be in the Sorbonne, Paris by Filhol (1888*a*: 144) and Stehlin (1903: 116).

Lophiodon cuvieri Watelet 1864 is a *nomen nudum*, as this author gave no figures or any information which can be construed as a description or even mention of a single distinguishing feature. The species must therefore take its authorship and date from Filhol (1888*a*).

RANGE of *L. cuvieri*. Early or middle Lutetian, D.D.R.; ?Lutetian, B.R.D. (see Tobien 1961) (*L.* cf. *cuvieri* from the Bartonian Gehlbergschichten of Helmstedt is thought to be reworked, see Russell *et al*., 1982: 13); middle to late Lutetian, ?Auversian, France; late Lutetian to ?Auversian, Switzerland; ?Auversian, Britain.

EMENDED DIAGNOSIS of *L. cuvieri* (translated and slightly modified from Fischer 1964; additions are italicized). Medium-sized species. Maxillary teeth large and rounded (*M^1 length 31 mm*). *Preultimate upper molars slightly broader than long.* Cingula reduced to a minimum. Upper molars with completely tapiroid metacone (the convexity on the outer wall is strong); the parastyle appears rounded and closely fitted to the paracone. *Upper premolars with or without small, poorly differentiated hypocone.* The base of the lingual side of the incisors mostly covered with very strong enamel wrinkles and papillae.

MATERIAL. Left M^3, not *in situ*, but almost certainly from the Elmore Member, Barton Clay Formation, foreshore at Elmore, near Lee-on-Solent, Hampshire. The specimen is in Gosport Museum (GM 978110–3) and a cast (M41977) in the BM(NH). Mr D.J. Kemp of Gosport Museum collected the specimen and presented the cast to the BM(NH).

DESCRIPTION. The tooth is moderately worn so that dentine is continuously exposed from parastyle to protocone and from ectoloph to hypocone. The mesial edge of the tooth is mainly missing as far back as the long axis of the protoloph, except for the buccal region of the parastyle and a small part at the mid-point of the mesial edge below the crown base.

Estimated maximum length perpendicular to the mesial edge is 38·5 mm. Maximum width parallel to the mesial edge is 41·7 mm. Measurements of M^3 from Filhol's (1888*a*) pl. 16, figs 3–4 of the syntype cranium of *L. cuvieri* are 36·4 mm long and 42·0 mm wide, so size and length/width ratio are very similar to this species.

The size, shape and proximity of the parastyle to the paracone is also similar to Filhol's figures of *L. cuvieri*. Only the buccal cingulum is slightly more extensive: it is weakly developed between the parastyle and paracone and is present buccal to the metacone, continuing distally to meet the distal cingulum.

Although M^3 in *Lophiodon* is less distinctive of the 'tapiroid' versus 'rhinocerotoid' condition than are the upper preultimate molars, the Elmore M^3 can be distinguished from that of most other similar-sized species as follows. In *L. isselense* it is relatively longer and narrower and the parastyle is separated from the paracone; in *L. tapiroides*, it is relatively longer and narrower and the parastyle, although no more detached than in *L. cuvieri*, is mesiodistally compressed. In *L. parisiense* it is very similar morphologically, although slightly but significantly smaller. *L. thomasi* from the French Bartonian is probably the species most similar to *L. cuvieri*, being distinguished only by the presence of a distinct P^4 hypocone. The unique holotype consists of an upper incisor, part of P^3?, complete P^4, and M^{1-2} only, so comparison with the Elmore M^3 is not possible. Whereas specific identity with either *L. cuvieri* or *L. thomasi* is equally possible, the determination as *L.* cf. *cuvieri* is considered the more practical alternative.

DISCUSSION. When Depéret (1906) first described *L. thomasi* from the Calcaire de Ducy of Sergy, Aisne, France (see Thomas 1906 for locality details), he distinguished it from *L. parisiense* by its P^4 hypocone, slightly less tapiroid M^{1-2} and slightly larger size. He did not compare it with *L. cuvieri*, from which it differs only in its distinct P^4 hypocone. Fischer (1964: 67, text-fig. 21) considered that *L. thomasi* was derived from *L. parisiense*, but *L. cuvieri* seems a better candidate for ancestry both morphologically and stratigraphically.

Stehlin (1903: 128–146) attributed various cheek teeth from Egerkingen to *L. cuvieri* or '*L. cuvieri*?'. Amongst these he described (1903: 135–136) several P^3s (as 'P^2') and P^4s (as 'P^1'), mainly from fissure α, as '*L. cuvieri*?' and as having incipient hypocones. They appear thus to form good morphological intermediates between *L. cuvieri* and *L. thomasi*, which, if phylogenetically intermediate, ought to be of Auversian age. Similar incipient hypocone development on P^2s and a P^3 attributed to *L. cuvieri* from the French Auversian locality of Arcis-le-Ponsart (Louis 1976: 50) would seem to confirm both the postulated ancestor–descendant relationship and an Auversian age for Egerkingen α. On the other hand, Sudre (1971: 92) noted beginnings of hypocone formation on a P^2 and P^3 of *L. cuvieri* from the late Lutetian (similar horizon to the types) of Pargny. So it would appear that large assemblages are necessary to account for individual variation (cf. Sudre, 1971, for *L. lautricense*). Upper premolars are eagerly awaited from the sparsely mammaliferous Elmore site.

Lophiodon cf. ***lautricense*** Noulet 1851

v. 1977*a* *Lophiodon* cf. *lautricense* Noulet; Hooker: 91–94.
v. *1980* *Lophiodon* cf. *lautricense* Noulet; Hooker & Insole: 43.

HOLOTYPE of *L. lautricense*. Mandible with broken teeth. Sables du Castrais; Braconnac, near Lautrec, Tarn, France (Muséum d'Histoire Naturelle de Toulouse, unnumbered).

RANGE of *L. lautricense*. Marinesian; France, Switzerland, West Germany.

DIAGNOSIS of *L. lautricense*. No formal diagnosis is available, but there are comprehensive accounts by Sudre (1971) and Stehlin (1903).

MATERIAL. Right symphysial fragment with roots of P_{2-3} and root and alveolus of P_4 (BGS GSM88617; cast in BM(NH), M31996). For details see Hooker (1977*a*).

Order **ARTIODACTYLA** Owen 1848*b*

Suborder **PALAEODONTA** Matthew 1929*b*

Superfamily **DICHOBUNOIDEA** Gill 1872
(rank emend. Viret 1961)

Family **DICHOBUNIDAE** Gill 1872 (*sensu* Sudre 1978*b*)

TYPE GENUS. *Dichobune* Cuvier 1822.

INCLUDED GENERA. *Protodichobune* Lemoine 1891; *Aumelasia* Sudre 1980; *Buxobune* Sudre 1978*b*; *Meniscodon* Rütimeyer 1888; *Mouillacitherium* Filhol 1882; *Hyperdichobune* Stehlin 1910*b*; *Metriotherium* Filhol 1882; *Synaphodus* Pomel 1848; *Messelobunodon* Franzen 1980*a*; ?*Lantianius* Chow 1964; ?*Chorlakkia* Gingerich, Russell, Sigogneau-Russell & Hartenberger 1979.

RANGE. Late Ypresian–Chattian, Europe; middle to late Eocene, Asia?

DIAGNOSIS. See Sudre (1978*b*: 18).

Genus ***HYPERDICHOBUNE*** Stehlin 1910*b*

TYPE SPECIES. *Dichobune spinifera* Stehlin 1906. Ludian, Entreroches, Canton Vaud, Switzerland.

INCLUDED SPECIES. *H. nobilis* (Stehlin 1906) Stehlin 1910*b*; *H. spectabilis* Stehlin 1910*b*; *H. hammeli* Sudre 1978*b*; ?*H. langi* (Rütimeyer 1891) Sudre 1972; *H*. sp. 1 and ?*H*. sp. 2 herein.

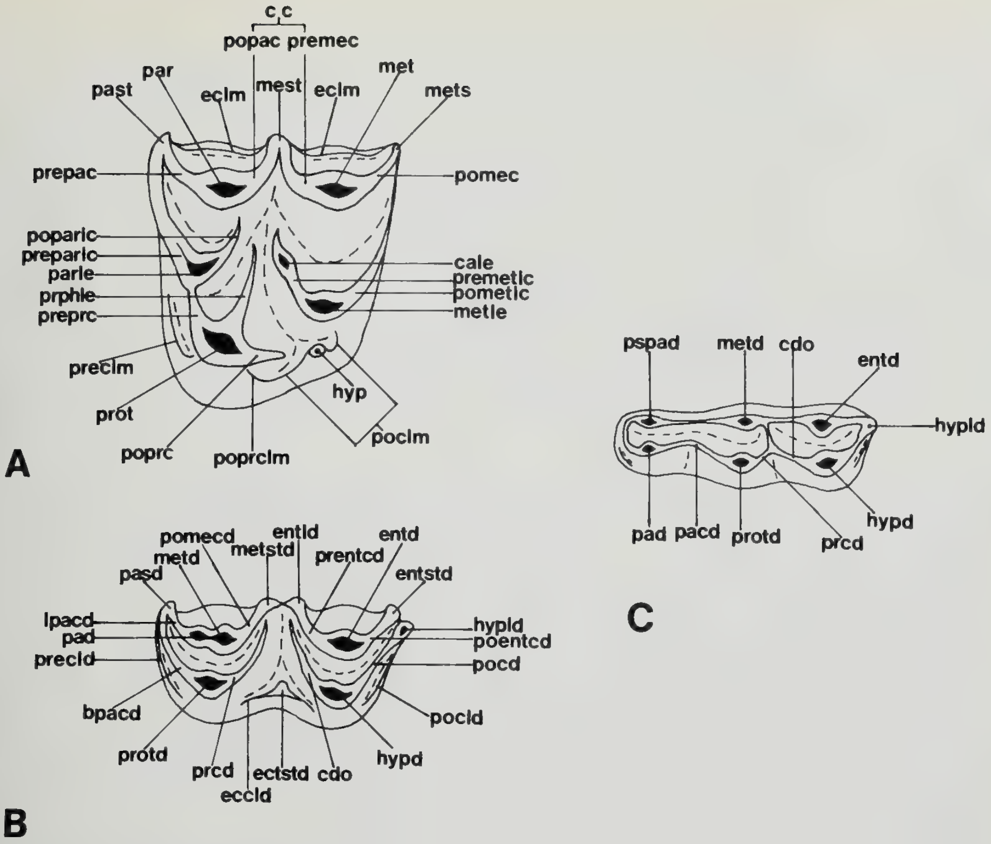
RANGE. M. Lutetian–Auversian, France; late Lutetian–late Ludian, Switzerland; Marinesian, England.

DIAGNOSIS. See Sudre (1978*b*: 35).

Hyperdichobune sp. 1
(Pl. 28; Table 29)

v. *1977b* ?*Hyperdichobune spectabilis* Stehlin; Hooker: 141.
v. *1980* *Hyperdichobune* sp.; Hooker & Insole: 43.

MATERIAL. P^4 (M36800); three $M^{1/2}$s (M36196, M37492, M37710); two M^3s (M37493–4); DP^4 (M37459); $M_{1/2}$ talonid fragment (M37553); M_3 (M36815); lower molar trigonid fragment ? (M36195); and DP_4 talonid fragment (M37496).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Text-figure 54 Dental nomenclature of artiodactyl cheek teeth, modified considerably from Coombs & Coombs (1977: 585, fig. 1). A, left upper molar; buccal edge towards top of page, lingual towards bottom. B, left lower molar, and C, left lower fourth deciduous premolar; buccal edges towards bottom of page, lingual edges towards top.

Abbreviations:

A. cale—central accessory conule
cc—centrocrista
eclm—ectocingulum
hyp—hypocone
mest—mesostyle
met—metacone
metle—metaconule
mets—metastyle
par—paracone
parle—paraconule
past—parastyle
poclm—postcingulum
pomec—postmetacrista
pometlc—postmetaconule crista
popac—postparacrista
poparlc—postparaconule crista
poprc—postprotocrista
poprclm—postprotocingulum
preclm—precingulum
premec—premetacrista
premetlc—premetaconule crista
prepac—preparacrista
preparlc—preparaconule crista
preprc—preprotocrista
prot—protocone
prphle—protolophule

B & C. bpacd—buccal paracristid
cdo—cristid obliqua
eccld—ectocingulid
ectstd—ectostylid
entd—entoconid
entld—entoconulid
entstd—entostylid
hypd—hypoconid
hypld—hypoconulid
lpacd—lingual paracristid
metd—metaconid
metstd—metastylid
pacd—paracristid
pad—paraconid
pasd—parastylid
pocd—postcristid
pocld—postcingulid
poentcd—postentocristid
pomecd—postmetacristid
prcd—protocristid
precld—precingulid
prentcd—pre-entocristid
protd—protoconid
pspad—pseudoparaconid
(of Hershkovitz, 1971).

Table 29 Length (l) and trigonid (w_1) and talonid (w_2) width measurements of teeth of *Hyperdichobune* sp. 1 from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1		w_2
M36800	RP^4	(3·7)		3·5	
M37710	$LM^{1/2}$	(4·1)		–	
M36196	$RM^{1/2}$	(4·5)		4·8	
M37493	LM^3	4·5		(5·0)	
M37494	RM^3	(4·8)		5·4	
M37492	$LM^{1/2}$	(4·5)		4·4	
M37459	RDP^4	(3·8)		(4·0)	
M37553	$RM_{1/2}$	–	–		3·3
M36815	RM_3	–	3·0		2·6
M37496	LDP_4	–	–		2·3

HORIZON AND LOCALITY. Creechbarrow Limestone Formation. Creechbarrow.

DESCRIPTION. P^4: The parastyle, base of paracone and preprotocrista are broken away. There is a large, distally-placed metacone two-thirds the size of the paracone. The distal cingulum is weak and swollen somewhat in the middle. An incomplete buccal cingulum is preserved round the metacone (Pl. 28, fig. 1). *H. spectabilis* from Entreroches (NMB Mt723) has a smaller metacone closer to the paracone; continuous buccal cingulum; stronger, more extensive distal cingulum with larger bulge forming incipient metaconule; and larger protocone with protolophule joining paracone.

$M^{1/2}$: M36196 is heavily worn and very weathered (Pl. 28, fig. 3). It has a large, distally skewed mesostyle; a strong buccal cingulum only between the mesostyle and metastyle; and apparently no lingual cingulum. It evidently had a fairly large hypocone which is completely fused by wear to the metaconule and protocone. The outline is somewhat oblique, the lingual cusps being slightly more mesial than the buccal cusps. Of M37710, only the lingual half remains (Pl. 28, fig. 6). The paraconule is small, close to the protocone, does not bulge mesially and there is a distinct postparaconule crista. The metaconule is nearly as large as the protocone and the hypocone is much smaller. What remains of the outline is similar to M36196. M37492 lacks the metaconal region, is smaller than M36196 or M37710 and may be an M^1 (Pl. 28, fig. 2). It is heavily worn but its development of lingual cusps is very similar to that of M37710. The mesial margin is straight and the parastyle is prominent. *H. spectabilis* M^{1-2} (Mt723) are similar in position of mesostyle, prominence of postparaconule crista and outline; but the hypocone is larger and there is a distinct mesial bulge to the paraconule.

M^3: M37493 (Pl. 28, fig. 7) is a very corroded tooth and thus difficult to compare character for character with M37494 (Pl. 28, fig. 4), whose parastylar area is broken. The latter, however, is slightly larger, seems to have a more rounded outline, stronger cingula and more mesially bulging paraconule. It is thus more like *H. spectabilis* than is M37493, whose paraconule is more like that of the $M^{1/2}$s, M37710 and M37492. Both M^3s have postparaconule cristae and no hypocone, but are relatively shorter teeth than the two known M^3s of *H. spectabilis* (Mt723 and Mt396, the latter figured by Stehlin, 1910*b*: 1100, text-fig. 225).

DP^4: Like M37492, M37459 has lost the metaconal region; it is quite worn, has thinner enamel and is lower-crowned than the molars; and it has a strong parastyle and postparaconule crista (Pl. 28, fig. 5). It appears to have been narrower mesially than distally and there is a strong cingulum round the more buccal protocone. It has more the proportions of the DP^4 of *Mouillacitherium* cf. *elegans* from Mormont (Stehlin 1906: pl. 12, fig. 30) than that of *H. spinifera* (*ibid.*: pl. 12, fig. 40).

$M_{1/2}$: This is very similar to the holotype M_{1-2} of *H. spectabilis*, but the hypoconulid is a larger, distally-projecting cusp and there is no crest joining the cristid obliqua to the entoconid (Pl. 28, fig. 10). The wear state of the two specimens is very similar.

M_3: The hypoconulid lobe is broken away and the tooth is very heavily worn (Pl. 28, fig. 11). The characters that remain visible are similar to *H. spectabilis* but like the $M_{1/2}$ there is no crest joining the cristid obliqua to the entoconid.

$M_{1/2/3}$: This doubtfully attributed trigonid fragment has a distinct paraconid slightly smaller than the metaconid but close to it (Pl. 28, fig. 9). Whether *H. spectabilis* had the same character is difficult to tell as the teeth are much more worn. However, the holotype M_3 has two deep areas of dentine separated by a shallower dentine isthmus; this suggests that intervening enamel had, at only a slightly earlier wear stage, separated a paraconid from a metaconid.

DP_4: This talonid fragment is like the $M_{1/2}$ but smaller, lower-crowned and with thinner enamel, its hypoconulid is more vertically orientated and its outline begins to taper mesially (Pl. 28, fig. 8).

DISCUSSION. Stehlin (1910*b*) could see no difference except size between *H. spinifera* and *H. spectabilis*, both from Entreroches. The only tooth types common to both, however, are P^4–M^1 and P_4–M_1. *H. spinifera* seems nevertheless to have an M^1 with paraconule not mesially salient and weaker cingula; a P^4 with a weaker incipient metaconule and better separated paracone and metacone and no protolophule; and a lower molar without a crest joining the cristid obliqua to the entoconid. From this evaluation and the above description, the Creechbarrow material appears to incorporate characters of both *H. spinifera* and *H. spectabilis*. This could mean that two species each related to those from Entreroches are represented, or that the morphological characters distinguishing the meagre sample of *H. spinifera* and *H. spectabilis* reflect intraspecific variation in a monospecific Creechbarrow assemblage, if not also in the Entreroches assemblages. More specimens are required to test these ideas.

The Creechbarrow teeth do not belong to either *H. hammeli*, *H. nobilis* or ?*H. langi*. The first has a narrower P^4 with small protocone and $M^{1/2}$ apparently with no postparaconule crista. The type series, however, appears to be composite: NMB Bchs430 with its large hypocone and overall arrangements of cusps (Sudre 1978*b*: text-pl. 1, fig. 5) fits the lipotyphlan *Amphilemur leemanni* (whose type locality, Bouxwiller, is the same as that of *H. hammeli*); also the absence of a P_4 hypoconid on the holotype makes it unlikely that the P^4 would have had subequal paracone and metacone like the paratype UM BUX66166 (Sudre 1978*b*: text-pl. 1, fig. 6).

Stehlin (1910*b*: 1101) distinguished *H. nobilis* from *H. spinifera* mainly on the former's less molariform referred P^4 (Stehlin 1906: pl. 12, fig. 25), in which it also differs from *H*. sp. 1.

?*H. langi* is a very different species which may not even belong to this genus (see below under ?*H*. sp. 2).

The $M^{1/2}$ from Lissieu, thought at first by Sudre (1972: 127, text-fig. 5C) to be *H. nobilis* and later (Sudre 1978*b*: 36) to be specifically indeterminate, is similar to the Creechbarrow molars, but from the figure appears to lack a postparaconule crista.

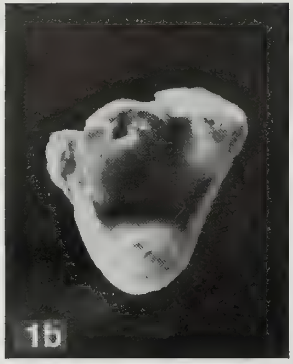
?***Hyperdichobune*** sp. 2
(Pl. 29, fig. 6)

v. *1977b* *Rhagatherium* sp.; Hooker: 141.
v. *1980* *Rhagatherium* sp.; Hooker & Insole: 44.

MATERIAL. Left $M^{1/2}$ (M37546), right $M^{1/2/3}$ lingual half (M36187); and doubtfully a right $M^{1/2}$ metaconal fragment (M37547).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. M37546 is triangular in outline, slightly broader than long, with the mesiobuccal corner a right angle. Outline and cusp pattern are very similar to *Mixtotherium* but with very small hypocone and a paraconule well separated from the protocone by a fissure. The centrocrista is buccally flexed and there is a large mesostyle. The paracone and metacone are buccally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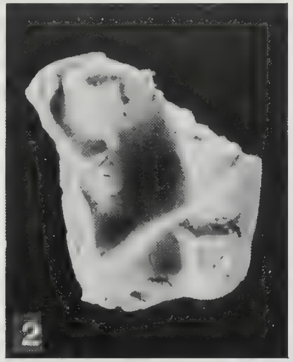
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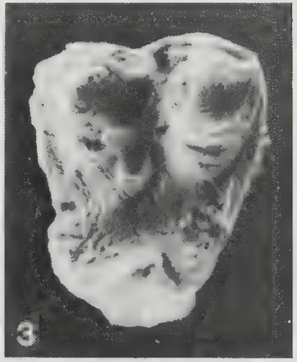
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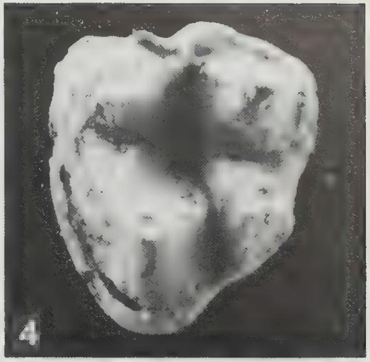
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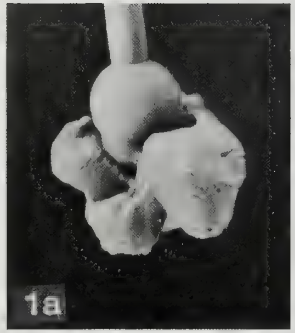
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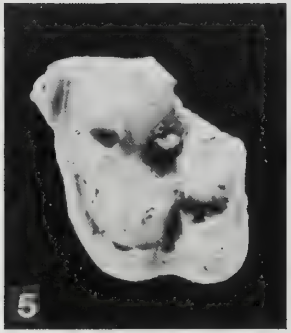
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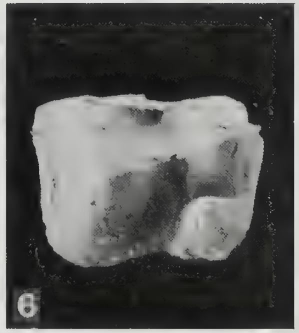
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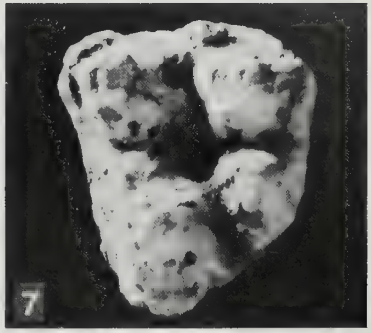
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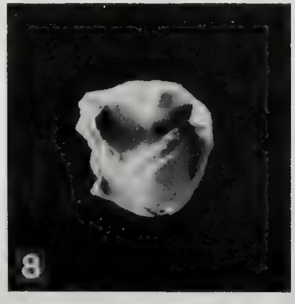
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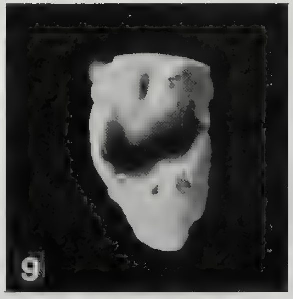
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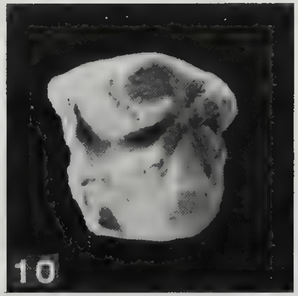
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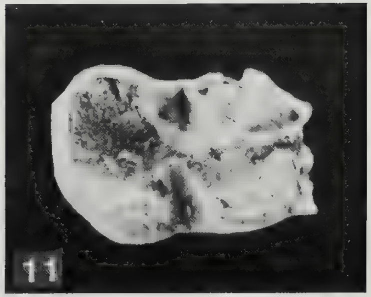
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salient and there is no buccal cingulum. The cusps generally appear gracile and are separated by broad deep valleys. The premetaconule crista is short, curving back to join the metacone mesiolingually. The tooth is 5·6 mm long and 6·1 mm wide.

In M36187, the hypocone is little more than a papilla at the distobuccal end of the postcingulum. M37547 shows the metastyle joined to the mesostyle by a buccal cingulum.

Discussion. The affinities are somewhat enigmatic. Strong similarities can be seen with ?*Hyperdichobune langi* from Egerkingen on the one hand and with *Mixtotherium* on the other. Decisions are hampered by only one tooth type being known for ?*Hyperdichobune* sp. 2. It could be doubted that ?*H. langi* is a *Hyperdichobune* for the following reasons. Firstly, on M^2 the near triangular outline tapers distally, the mesiobuccal corner being acute; second, the upper molar paraconule is large and well separated from the protocone; and third, on the upper molars the very weak postparaconule crista is directed towards the mesostyle, not towards the middle of the paracone.

No premolars were recorded for '*Dichobune*' *langi* by Stehlin (1906: 623–625), nor did he (1910*b*) refer it with the other three species to his new genus *Hyperdichobune*. Sudre (1972: 121–126, text-figs 3–4) referred upper and lower molars from Lissieu to the species and included it in *Hyperdichobune* on the basis of an isolated P^3. The P^4 was later considered (Sudre 1978*b*: 36) to be wrongly identified and to require replacing by another one that he had referred to *H. nobilis* (Sudre 1972: 127, text-fig. 5B). The latter tooth is like P^4 of *Mixtotherium* in its more sharply triangular outline, buccal cingulum round the metacone, large, mesially salient parastyle and small paraconule and metaconule. If it really belongs to ?*H. langi*, it suggests a close relationship with *Mixtotherium*; alternatively it may belong to *Mixtotherium infans*.

?*H. langi* M^2 differs from that of ?*H.* sp. 2 from Creechbarrow mainly in being smaller, relatively shorter and having a larger hypocone. *Mixtotherium* differs from ?*H.* sp. 2 in having a strong buccal cingulum, less buccally salient paracone and metacone, the paraconule fused to the protocone and no hypocone. The intermediate state of ?*H.* sp. 2 suggests affinities between ?*H. langi* and *Mixtotherium* and possible derivation of the latter from the Dichobunidae. The absence of either premolars associated with molars or of any known basicranial in ?*H. langi* means that we do not know whether any of the other distinctive features of *Mixtotherium*, such as absence of mastoid exposure, had already evolved in these dichobunids. When better known a new generic name may be found necessary for ?*H. langi* and ?*H.* sp. 2.

Family **MIXTOTHERIDAE** Pearson 1927

Type and only known genus. *Mixtotherium* Filhol 1880*b*. See also comments under ?*Hyperdichobune* sp. 2, above.

Genus ***MIXTOTHERIUM*** Filhol 1880*b*

(Complicated synonymy dealt with by Stehlin, 1908: 799–828).

Type species. *M. cuspidatum* Filhol 1880*b*. Phosphorites du Quercy; France (figured Filhol, 1882: pl. 9, figs 1–7).

Included species. *M. gresslyi* Rütimeyer 1891 (including *M. priscum* Stehlin 1908); *M. infans* Stehlin 1910*b*; *M. leenhardti* Stehlin 1908; *M. depressum* (Filhol 1884) Stehlin 1908; *M. quercyi* (Filhol 1888*b*) Stehlin 1908.

Plate 28 Light macrographs of cheek teeth of *Hyperdichobune* sp. 1 from Creechbarrow, × 9. Occlusal views, except Fig. 1a. Fig. 1a, b, right P^4 (reversed) (M36800). a, buccal and b, occlusal views. Fig. 2, left $M^{1/2}$ (M37492). Fig. 3, right $M^{1/2}$ (reversed) (M36196). Fig. 4, right M^3 (reversed) (M37494). Fig. 5, right DP^4 (reversed) (M37459). Fig. 6, lingual half of left $M^{1/2}$ (M37710). Fig. 7, left M^3 (M37493). Fig. 8, talonid fragment of left DP_4 (M37496). Fig. 9, trigonid fragment of right $M_{1/2/3}$ (reversed) (M36195). Fig. 10, talonid fragment of right $M_{1/2}$ (reversed) (M37553). Fig. 11, right M_3 with broken hypoconulid lobe (reversed) (M36815). See p. 376.

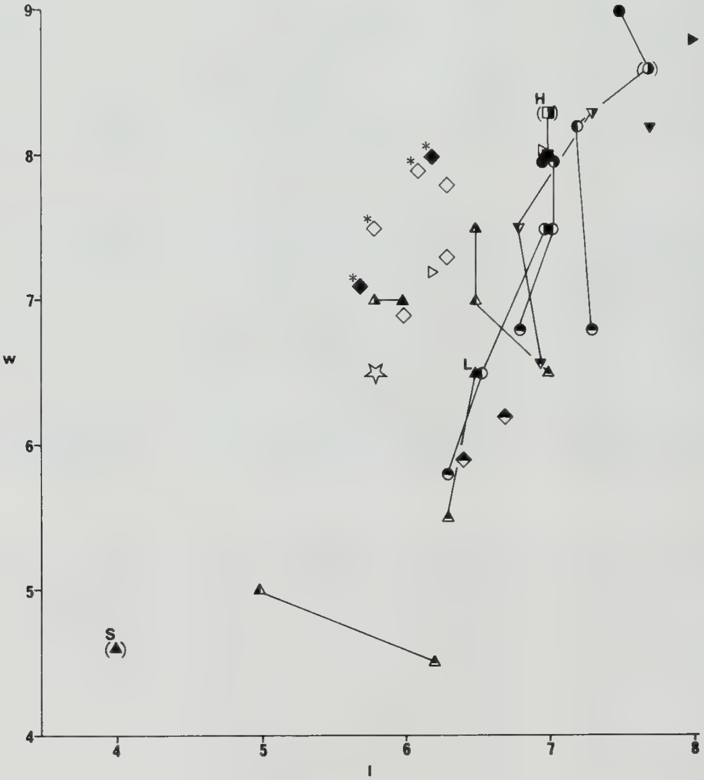
RANGE. Late Lutetian–Ludian; England, France and Switzerland.

DIAGNOSIS. See Viret (1961: 902).

DISCUSSION. This genus is very local in occurrence, being almost entirely restricted to the fissure deposits of Switzerland and France, although it is not uncommon where it occurs. It was recently discovered in the Upper Calcaire Grossier of the Paris Basin (Ginsburg *et al.* 1977) and the Creechbarrow records are the first for England. It has been found in the recent excavations in Le Quercy at the early Ludian sites of La Bouffie and Perrière (Crochet *et al.* 1981).

Once considered related to anoplotheres or anthracotheres, the genus has sometimes been included in the Cebochoeridae (e.g. Sudre 1972; Simpson 1945) because of superficially similar skull shape and lack of mastoid exposure; its possible relationships with the dichobunids are discussed herein under *Hyperdichobune* above.

Of the described species, only *M. cuspidatum*, *M. gresslyi* and *M. infans* are well characterized. *M. quercyi* and *M. depressum* appear very close to typical *M. cuspidatum*, whilst *M. leenhardti* and *M. priscum* are difficult to separate from *M. gresslyi*. *M.* cf. *priscum* and *M.* cf. *gresslyi* from Mormont and Quercy were tentatively separated by Stehlin (1908) from the typical assemblages of these species on stratigraphical, not morphological grounds. It is prob-



Text-figure 55 Scatter diagram of length (l) against width (w) in P^4–M^3 of *Mixtotherium*. □ = *M.* '*priscum*' Stehlin from Egerkingen Huppersand; ▽ = *M.* '*priscum*' from Egerkingen γ; △ = *M. gresslyi* Rütimeyer and *M. infans* Stehlin from Egerkingen α; ◁ = *M.* '*priscum*' from Lissieu; ○ = *M.* 'cf. *priscum*' from the Phosphorites du Quercy; ◇ = *M.* aff. *gresslyi* from Creechbarrow; ☆ = *M.* 'cf. *gresslyi*' from Mormont. ∗ indicates specimens where the parastyle is broken. H = holotype of *M. priscum*; L = lectotype of *M. gresslyi*; S = syntype of *M. infans*. Symbols solid above = P^4; solid on left = M^1; solid on right = M^2; completely solid = M^3; and outline = $M^{1/2}$. Measurements in millimetres. Lines join teeth of one individual.

able that the slightly deeper horizontal mandibular ramus of *M. leenhardti* (Stehlin 1908: text-fig. 129) could result from old age of the individual, as the teeth appear quite worn, compared for instance to his text-fig. 131 of *M.* cf. *priscum*. Gaining an accurate idea of the range of intraspecific variation in this genus is difficult in view of the small number of specimens and the poor locality and stratigraphical data for the old Quercy material. The larger collections from Egerkingen, including those from Egerkingen γ made after Stehlin's publication of *Mixtotherium*, offer better potential. The Creechbarrow material, although not including osteological parts, consists of enough teeth to demonstrate variation for a number of features. A revision of the complete genus is highly desirable.

From the scatter diagram (Text-fig. 55), the Creechbarrow material makes a plot intermediate between *M. gresslyi* and *M. priscum* according to Stehlin's concepts. However, Stehlin (1908: 822) also thought that *M. priscum* might in the light of further material be divided into two or three species. He was struck by its high morphological variation. He could not convincingly separate it morphologically from *M. gresslyi* except by referring the very small individual from Egerkingen α (NMB Eg159; Stehlin 1910*b*: pl. 17, fig. 21), with more quadrate M^1 and elongated P^4, to the latter species. In Text-fig. 55, Eg159 plots closer to the figured syntype M^3 of *M. infans* than to the type M^1 of *M. gresslyi*. Sudre (1972: 133–134, fig. 9) described and figured *M. gresslyi* from Lissieu, but in size his material (isolated upper molars) is close to Eg159 and *M. infans*. His figures suggest that in morphology it differs too; its high selenodonty, deeply incised parastyles and in one case (1972: fig. 9c) absence of paraconule more closely resemble the xiphodont *Haplomeryx*. Text-fig. 55 shows no clear size difference between *M. gresslyi* and *M. priscum* if one excludes Eg159. *M. priscum* from Egerkingen α can easily be accommodated within *M. gresslyi*, whose type is from the same fissure. The assemblages of *M. priscum* from Egerkingen Huppersand (grey marl facies) and Egerkingen γ appear slightly larger, but more specimens would almost certainly produce a normal range overlapping extensively with *M. gresslyi*. The differences are no greater than would be expected from assemblages of one species from different localities or slightly different stratigraphical horizons. It is proposed here that the species *M. priscum* be synonymized with *M. gresslyi*, whilst recognizing that a subspecific difference might be demonstrated if a systematic study of the Egerkingen material were undertaken. Table 30 compares coefficients of variation of various combinations of the different assemblages. The Creechbarrow assemblage (here referred to as *M.* aff. *gresslyi*) is intermediate in size between the Egerkingen γ/Huppersand assemblages ('*M. priscum*') and the Egerkingen α assemblage (type *M. gresslyi*). It is possibly closer to the latter.

Mixtotherium aff. ***gresslyi*** Rütimeyer 1891
(Pl. 29, figs 1–4; Pl. 30; Text-fig. 55; Tables 30–33)

v. *1977b* *Mixtotherium priscum* Stehlin; Hooker: 141.
v. *1980* *Mixtotherium priscum* Stehlin; Hooker & Insole: 44.

LECTOTYPE of *M. gresslyi* (following Sudre 1972: 133, as 'type'). Right maxillary fragment with P^2–M^1. Auversian, Egerkingen α; Canton Solothurn, Switzerland (figured Rütimeyer 1891: pl. 6, fig. 1 and Stehlin 1908: 817, text-fig. 129).

Table 30 Coefficients of variation (v) for length of $M^{1/2}$ in *Mixtotherium* assemblages. N = number of specimens.

Assemblages	N	v
M. gresslyi and *M.* '*priscum*' from Egerkingen α	4	5·53
Ditto and *M.* 'cf. *gresslyi*' from Mormont	5	6·16
Ditto and *M.* aff. *gresslyi* from Creechbarrow	11	4·68
Ditto and *M.* '*priscum*' from Egerkingen γ and Huppersand	14	7·34
M. '*priscum*' from Egerkingen γ and Huppersand and *M.* aff. *gresslyi* from Creechbarrow	9	8·04
M. aff. *gresslyi* from Creechbarrow	6	3·19

Material. Two P^3s, broken mesially (M37505, M37559); two P^4s (M37506–7); five $M^{1/2}$s, one fragmentary (M36184, M37509–10, M37514, M37512); seven M^3s, three fragmentary (M36185–6, M37508, M37515, M37511, M37513, M37516); three fragmentary upper molars (M36818, M37517–8); two $P_{2/3}$ talonid fragments (M36438, M37560); two P_3s lacking mesial half (M36797, M37558); two P_4s lacking talonids (M37519–20); seven $M_{1/2}$ talonid fragments (M36193, M36796, M36809–10, M37522–4); two M_3 talonid fragments (M36408, M36500); nine lower molar trigonid fragments (M36188–9, M36198, M36827, M37521, M37525–7, M37711); two DP_2? fragments (M36416, M36808); DP_3? talonid fragment (M36194); two DP_4 trigonid fragments (M36411, M37550).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Range of the species (including aff. and cf.). Late Lutetian, France and Switzerland; Auversian, Switzerland; Marinesian, England and Switzerland; and ?Marinesian and Ludian, France.

Emended diagnosis of species. Medium-sized species (mean length of $M^1 = 6·5$ mm); upper molars broader than long (length *c.* 80% of width); depth of adult mandibular ramus beneath the distal end of M_3 2·5 times length of M_3.

Differential diagnosis. *M. cuspidatum* is larger; has upper molars with approximately equal length and width; and deeper mandible. *M. infans* is smaller.

Table 31 Length (l) and width (w) measurements of upper teeth of *Mixtotherium* aff. *gresslyi* from Creechbarrow. Measurements in millimetres. *indicates parastyle missing.

No.	Tooth	l	w
M37505	RP^3	–	3·9
M37559	RP^3	–	4·0
M37506	LP^4	6·7	6·2
M37507	RP^4	6·4	5·9
M36184	$LM^{1/2}$	6·0	6·9
M37509	$LM^{1/2*}$	6·1	7·9
M37510	$LM^{1/2*}$	5·8	7·5
M37514	$RM^{1/2}$	6·0	–
M36185	LM^3	6·3	7·3
M37508	LM^{3*}	5·7	7·1
M37515	LM^{3*}	6·2	8·0
M36186	RM^3	6·3	7·8

Table 32 Trigonid (w_1) and talonid (w_2) width measurements of lower teeth of *Mixtotherium* aff. *gresslyi* from Creechbarrow. It was not possible to measure length in any of these teeth. Measurements in millimetres.

No.	Tooth	w_1	w_2
M36438	$LP_{2/3}$	–	3·0
M36797	LP_3	–	3·5
M37558	LP_3	–	3·5
M37560	RP_3	–	2·7
M37519	LP_4	3·4	–
M37520	RP_4	3·4	–
M36796	$LM_{1/2}$	–	4·5
M37522	$LM_{1/2}$	–	4·2
M36193	$RM_{1/2}$	–	4·1
M36809	$RM_{1/2}$	–	3·6
M37523	$RM_{1/2}$	–	3·8
M37524	$RM_{1/2}$	–	4·7
M36500	LM_3	–	4·5
M36189	$LM_{1/2/3}$	4·0	–
M37521	$LM_{1/2/3}$	4·2	–
M37525	$LM_{1/2/3}$	4·0	–
M37526	$LM_{1/2/3}$	4·5	–
M36188	$RM_{1/2/3}$	4·1	–
M37527	$RM_{1/2/3}$	4·2	–
M37711	$RM_{1/2/3}$	3·9	–
M36808	LDP_2?	2·0	–
M36416	RDP_2?	1·9	–
M36194	LDP_3?	–	2·7
M37550	RDP_4	3·0	–

DESCRIPTION. Comparison is made with a maxilla from the Quercy Phosphorites (M33522), casts of a maxilla (NMB Eh409) and mandibular ramus (Eh424) from Egerkingen γ and original M^3 (M12017), mandibular ramus (M12015) and M_3 (M12016) from Egerkingen undifferentiated (although the ochreous sandy bolus matrix suggests fissure γ also); as well as with Stehlin's figures (1908, 1910*b*).

P^3: Both teeth are broken mesially through the paracone. Their metacone is larger and better separated from the paracone than on Eh409 and M33522. In fact the metacone is nearly as large as the paracone. The protocone is also larger in M37559 than on these two and M37505.

P^4: Both have strongly buccally flexed centrocristae and strong mesostyles – more so than M33522. There is a strong buccal cingulum on M37506 behind the mesostyle, which broadens the stylar shelf and pushes the metacone further from the buccal margin than is the case in M37507. In the latter the buccal cingulum is restricted to the mesial side of the metastyle. The metaconule is larger in M37507 and has a premetaconule crista joining it to the metacone at a mesiolingual position. The parastyle is more mesially salient in M37506 than M37507. Both have overall smaller parastyles than M33522.

Upper molars: See Table 33 for the distribution of the main variable characters. There is a partial positive correlation between length of the premetaconule crista and the proximity of the paraconule to the protocone; otherwise the characters appear randomly distributed. There is nothing to suggest that more than one species is represented. M^3 can generally be distinguished from M^1 or M^2 (when absence of a recognizable distal interstitial facet is unreliable), by being relatively longer and having a more lingually displaced metacone.

P_{2-3}: Two specimens from Egerkingen γ show P_3 to be very variable in this assemblage. One (M12015) resembles the P_2 of another (Eh424) in the small size of the hypoconid, absence of a metaconid and shallow lingual concavity of the protoconid–paraconid–parastylid crest. The P_3 of Eh424, on the other hand, has a small distolingual metaconid joined to the protoconid by an oblique protocristid; the larger hypoconid is slightly displaced buccally; and the protoconid–paraconid–parastylid crest is more deeply concave lingually. On this basis, the distal fragment (M36438) from Creechbarrow could be either a P_2 or a simple P_3. Size favours it being a P_2. On this basis, it could also be argued that the equal-sized M37560 (also a distal fragment), with a small metaconid close mesiolingually to the hypoconid, might be a complex P_2 rather than a P_3. M36797 and M37558 are convincing P_3s. They are better preserved but still incomplete mesially. Both have equal-sized metaconids which lie equidistantly distolingual to the protoconid and mesiolingual to the hypoconid, but, unlike Eh424, displaced from the lingual tooth edge and with distolingual oblique crests. The hypoconid on M37558 is smaller than on M36797 and the same size as the metaconid. The cristid obliqua lives up to its name on M36797 (as on Eh424) but is near longitudinal on M37558.

P_4: Both are trigonid fragments which show a buccal paraconid opposite a large lingual pseudoparaconid and a buccally concave paracristid. The specializations here are thus reminiscent of those of an artiodactyl DP_4. That these are not DP_4s is corroborated by enamel thickness and the presence at Creechbarrow of two DP_4s referable to this species. One of the latter is complete enough to show a better divided mesial lobe with the pseudoparaconid larger than the paraconid. Stehlin (1908: 826–7; 1910*b*: pl. 20, figs 4, 12–13, 47) had some problems distinguishing between the two tooth types. Identification of Ef209 as a DP_4 was based on narrower outline and pseudoparaconid higher than paraconid. Whether the morphology of the Creechbarrow P_4s occurs in *M. gresslyi* from Egerkingen depends on whether Stehlin's (1910*b*: pl. 20, fig. 47) enigmatic tooth (NMB Ef238) is a P_4 or DP_4. However, Ef238 has a pseudoparaconid larger than the paraconid, not the other way round, and it could be argued that the Creechbarrow specimens are constant for this character. There is a slight difference in size of the parastylid between the two Creechbarrow P_4s, but otherwise they are remarkably similar.

Lower molars: These are all fragmentary, mainly having been broken into trigonid and talonid parts. The parastylid varies somewhat in strength (Pl. 30, figs 7–8); in two specimens it

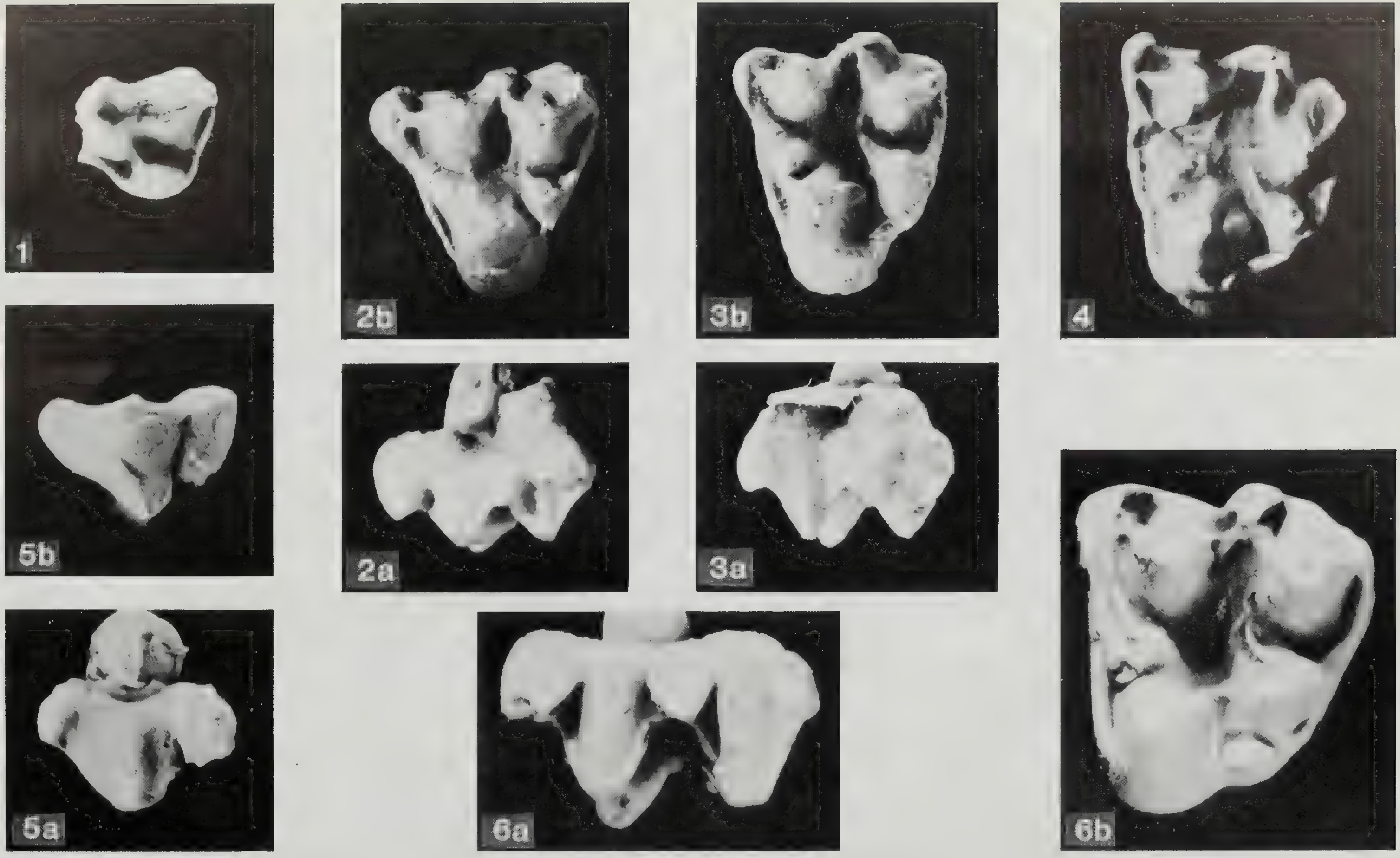


Plate 29 Light macrographs of upper cheek teeth of *Mixtotherium* aff. *gresslyi* Rütimeyer, ?*Mixtotherium* sp. indet. and ?*Hyperdichobune* sp. 2, from Creechbarrow. Views are buccal (a) and occlusal (b or unsuffixed).

Figs 1–4 *Mixtotherium* aff. *gresslyi* Rütimeyer, × 5·5. Fig. 1, right P^3 (reversed) (M37505). Fig. 2a, b, left P^4 (M37506). Fig. 3a, b, left $M^{1/2}$ (M36184). Fig. 4, left M^3 (M36185). See p. 383.

Fig. 5a, b ?*Mixtotherium* sp. indet. Left DP^3? (M36813), × 9. See p. 389.

Fig. 6a, b ?*Hyperdichobune* sp. 2. Left $M^{1/2}$ (M37546), × 8. See p. 379.

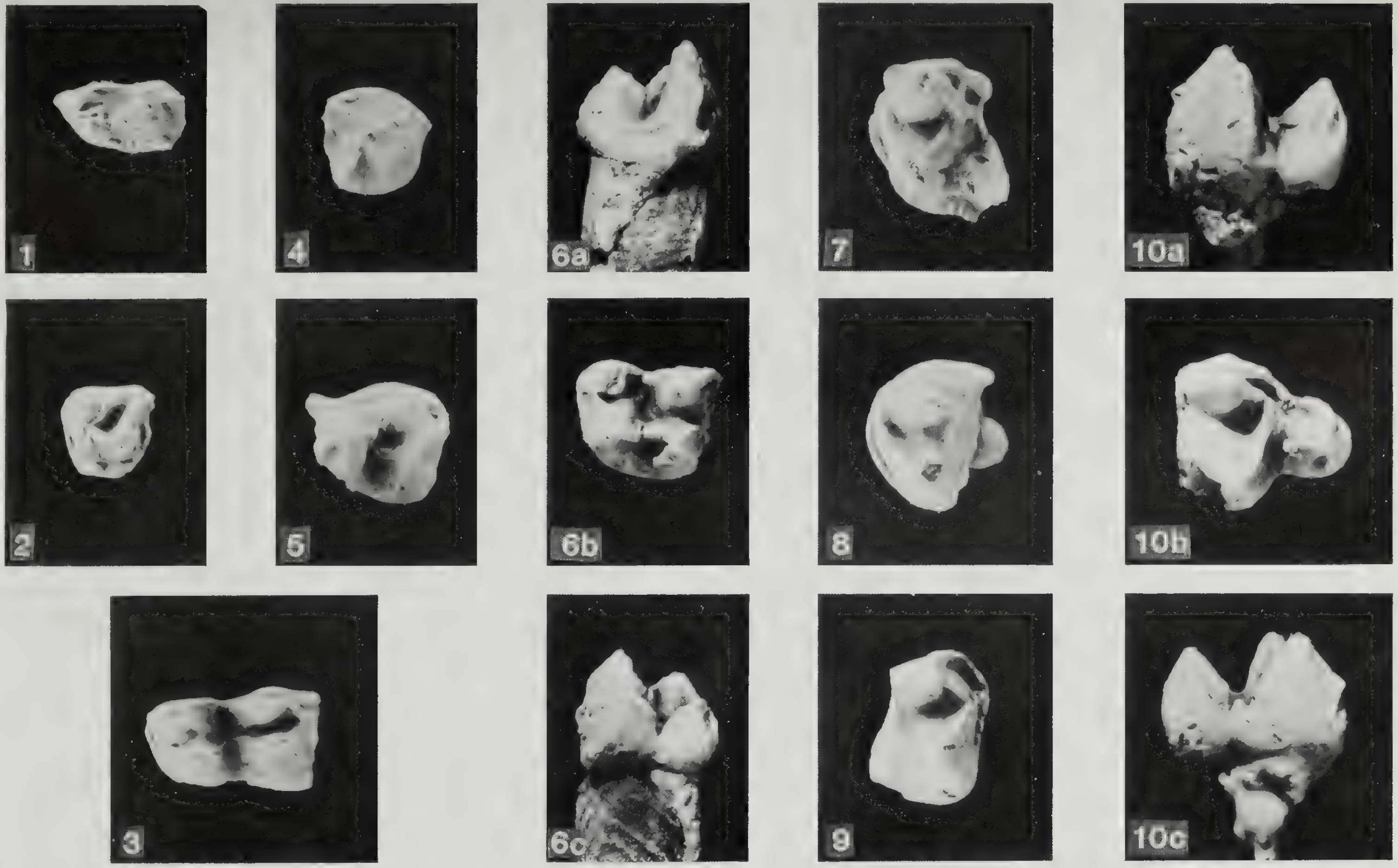


Plate 30 Light macrographs of lower cheek teeth of *Mixtotherium* aff. *gresslyi* Rütimeyer from Creechbarrow, × 5·5. Views are buccal (a), occlusal (b or unsuffixed) and lingual (c). Fig. 1, left DP_2 (M36808). Fig. 2, left DP_3 (M36194). Fig. 3, right DP_4 trigonid fragment (reversed) (M37550). Fig. 4, left P_2? talonid fragment (M36438). Fig. 5, left P_3 broken mesially (M37558). Fig. 6a–c, left P_4 (M37519). Fig. 7, left $M_{1/2/3}$ trigonid fragment (M37525). Fig. 8, left $M_{1/2/3}$ trigonid fragment (M37526). Fig. 9, left $M_{1/2}$ talonid fragment (M37522). Fig. 10a–c, left M_3 talonid fragment (M36500). See p. 383.

Table 33 Distribution of intraspecifically variable characters in upper molars of *Mixtotherium* aff. *gresslyi* from Creechbarrow.

No.	Tooth	mesostyle loop	extent of premetaconule crista as fraction of distance from metaconule to mesostyle	distance of paraconule from protocone as fraction of distance from protocone to paracone	extent of lingual cingulum	extent of post-cingulum	extent of buccal cingulum
M36184	$M^{1/2}$	open	$>\frac{1}{2}$	$\frac{2}{5}$	postproto-cingulum	just to metaconule	absent parastyle–mesostyle
M36190	$M^{1/2}$	open	–	–	–	–	–
M37509	$M^{1/2}$	widely open	$\frac{1}{3}$	$\frac{1}{3}$?	postproto-cingulum	$\frac{1}{2}$ round metaconule	–
M37510	$M^{1/2}$	narrowly open	$\frac{1}{2}$	$\frac{2}{5}$	postproto-cingulum	just to metaconule	continuous
M37512	$M^{1/2}$	–	–	$\frac{1}{3}$?	round protocone	all round metaconule	–
M37514	$M^{1/2}$	closed	*c.* $\frac{1}{2}$	–	–	–	between parastyle and adjacent stylar cuspule
M36185	M^3	widely open	$\frac{1}{2}$	$\frac{2}{5}$	postproto-cingulum	$\frac{1}{2}$ round metaconule	absent parastyle–mesostyle
M36186	M^3	widely open	$<\frac{1}{2}$	$\frac{1}{3}$	round protocone	$\frac{1}{2}$ round metaconule	?absent parastyle–mesostyle
M37508	M^3	closed	$\frac{1}{3}$	$\frac{1}{3}$	–	–	continuous
M37511	M^3	open?	$>\frac{1}{2}$	–	–	just to metaconule	–
M37513	M^3?	open	$<\frac{1}{2}$	–	–	–	broken in front of mesostyle
M37515	M^3	widely open	$\frac{1}{3}$	$\frac{1}{3}$	postproto-cingulum	–	broken at least behind mesostyle
M37517	$M^{1/2/3}$	–	$\frac{1}{3}$?	–	postproto-cingulum	$\frac{1}{2}$ round metaconule	–
M37518	$M^{1/2/3}$	–	–	–	postproto-cingulum	just to metaconule	–

is nearly as weak as in the *M. gresslyi* specimens from Egerkingen γ. A typical character of *Mixtotherium* M_{1-2}s is the presence of a distal cingulum which loops round the distolingual corner of the tooth from the hypoconid to run up the distal wall of the entoconid. On some Creechbarrow specimens it is joined to the postcristid by a median to near lingual crestiform hypoconulid; on all the specimens the lingual limb of the postcristid is present although it may not reach the tip of the entoconid (sometimes missing on *M. cuspidatum*); on one specimen the distal cingulum does not extend buccally from the hypoconulid.

DP_2?: Only mesial fragments are preserved. They are similar to Stehlin's figured DP_4 from Mormont (see p. 385) but are narrower and the metaconid appears to have been absent. M36808 has a parastylid which is slightly smaller than the paraconid and is situated mesiolingually to it. An extra small stylar cusp occurs mesial to the parastylid and makes the mesial outline taper to a point. The buccal cingulum is papillate and the lingual cingulum is weak and interrupted. M36416 is broken mesially as well as distally but seems to be beginning to broaden just before the mesial truncation. A very small cusp at the level of the non-existent lingual cingulum and distolingual to the large protoconid may represent the metaconid. A steep longitudinal protocristid bypasses it and is truncated by the distal breakage (cf. Stehlin 1910*b*: pl. 20, fig. 24).

DP_3: M36194 is lower-crowned and has thinner enamel than the P_3s. It has a similar arrangement of cusps but the postcristid reaches the lingual margin at a small entoconid with a sharp distal crest; the cristid obliqua is only slightly oblique; and what is preserved of the confluent distal and buccal cingula is strong and papillate. Compared with the DP_3 that Stehlin figured from Mormont (1910*b*: 1116, text-fig. 231) the metaconid appears to extend further lingually and the cingula appear stronger, but the figure is not clear on the latter point.

DP_4: M37550 is a trigonid fragment which differs from Stehlin's (1910*b*: pl. 20, fig. 12) figure in its more transverse relationship between the protoconid and metaconid and is slightly narrower in outline. M36411 is more fragmentary but shows the protoconid and metaconid to have a more oblique relationship than Stehlin's specimen. Variation appears to be high in this tooth.

DISCUSSION. It is difficult to judge the significance of the more obvious differences between the Creechbarrow assemblage and the various Egerkingen assemblages. The relative constancy of the position of the P_3 metaconid, the large P^3 metacone and the P_4 paraconid lobe, the last two perhaps being linked by occlusal relationships, suggest specializations in the Creechbarrow assemblage. Some evidence for variation in these characters in *M. gresslyi* and *M. cuspidatum*, however, demands a cautious approach. A statistical study of the genus could be enlightening.

?***Mixtotherium*** sp. indet.

(Pl. 29, fig. 5)

MATERIAL. Left DP^3? (M36813).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. Length is 3·6 mm. The outline is wedge-shaped, the enamel thin, and the tooth is fairly worn and broken distolingually where a protocone was probably once present. The paracone is by far the largest cusp. The parastyle is large and buccally as well as mesially salient. The metacone is very small and only lingually salient, a feature increased by wear from the hypoconid of a ?DP_3. The distal third of the buccal edge bulges and is bent buccally. A weak mesiolingual cingulum is raised high on the flank of the paracone.

This tooth differs from the DP^3 of *Mixtotherium cuspidatum* figured by Stehlin (1908: 803, text-fig. 120) in being much smaller and less molariform. The latter has a mesostyle, a large metacone and a crest joining the metacone to the protocone. Evidence for possible attribution of the Creechbarrow specimen to *Mixtotherium* comes from a referred DP^3 of *M.* '*priscum*' (= *M. gresslyi*, see p. 383) from Egerkingen γ (NMB Eh414). This tooth is associated in a maxillary fragment with a DP^4 which is likewise far less molariform than that of *M. cuspidatum*. The Egerkingen γ DP^3 is very similar to M36813. It differs in being nearly twice the linear size; in having a straighter buccal edge with a buccal cingulum bordering the metacone; and in having a lower mesiolingual cingulum.

The size of M36813 would be appropriate to that of *M. infans* but no DP^3s have been attributed to this species. Specific identification based on this single tooth would be unreliable.

Family **CEBOCHOERIDAE** Lydekker 1883

TYPE GENUS. *Cebochoerus* Gervais 1852.

INCLUDED GENERA. *Acotherulum* Gervais 1850 (?including *Moiachoerus* Golpe-Posse 1972, *fide* Sudre 1978*b*: 82) and Gen. nov. (for *Choeromorus* Gervais 1852, *sensu* Jaeger 1971).

RANGE. Middle Lutetian to early Stampian, Europe.

DIAGNOSIS. See Sudre (1978*b*: 49).

INTRODUCTION. This small family has long been the subject of discussion over generic content and nomenclatural priorities (e.g. Stehlin 1908, Depéret 1917, Pearson 1927, Sudre 1978*b*). The main causes of these problems are the rather low anatomical diversity (taxonomic differences often being minor and easily confused with intraspecific variation) and the poor quality or loss of type specimens. A preoccupation with increase in size as the main criterion in the recognition of lineages has also impeded the unravelling of the morphological details of the group.

The problem of the genus *Choeromorus* (*sensu* Stehlin 1908), whose only difference from *Cebochoerus* was supposed to be the presence of enlarged pig-like lower canines and extrapolated small first premolars, was essentially overcome by Sudre (1978*b*: 52–54); he considered the affinity of the canines, which were isolated, with the Cebochoeridae to be unproven and that the problem therefore never really existed. The probability that these teeth belong to palaeotheres is discussed herein above under *Lophiotherium* (p. 352).

The problem caused by synonymy of the type species of *Cebochoerus* and *Acotherulum* was discussed by Sudre (1978*b*: 49–51). He proposed the changing of the type species of *Cebochoerus* to *C. lacustris* (following the apparent sentiments of Gervais (1859: 198)) in order to stabilize the Cebochoeridae type genus and to maintain its 'common usage' distinction from *Acotherulum*. No formal proposal has yet been made to the ICZN regarding this change of type species. Sudre's separation of the two genera is followed here, but a different content of species for each is shown to be necessary. It is worthy of note that the holotype of *C. anceps* is no longer missing (as recorded by Depéret 1917: 102 and Sudre 1978*b*: 50) but is in the collections of the University of Lyon (FSL 6796).

Genus ***CEBOCHOERUS*** Gervais 1852 (*sensu* Gervais 1859)
[incl. *Cebochoerus* (*Gervachoerus*) Sudre 1978*b* in part]

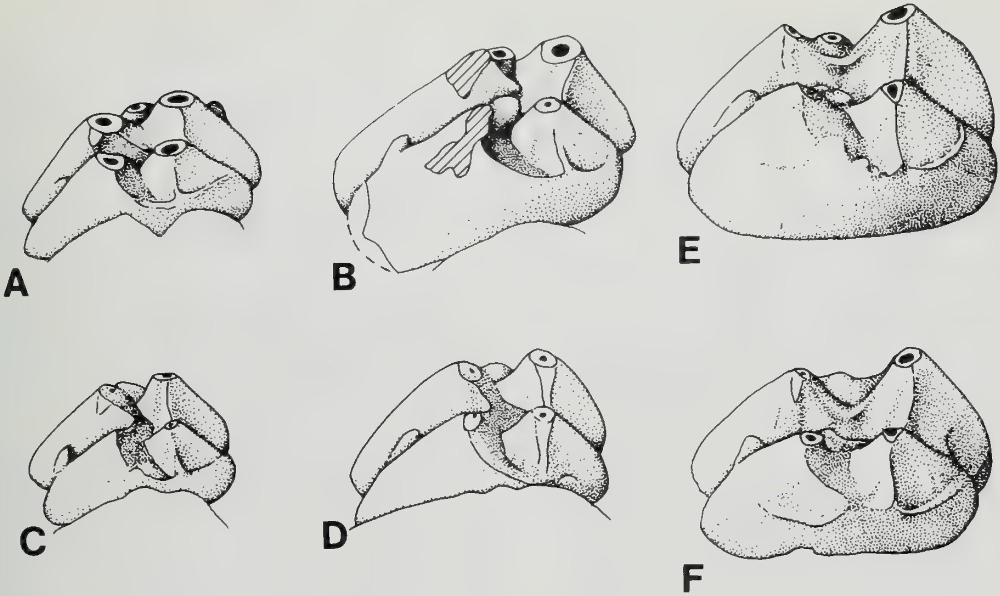
TYPE SPECIES. *C. anceps* Gervais 1852. Ludian; La Débruge, Vaucluse, France. This is pending formal application to the ICZN for change of type species to *C. lacustris* Gervais 1856 (from the Ludian limestone of Souvignargues, Gard, France), the holotype of which was reported lost by Sudre (1978*b*: 74).

INCLUDED SPECIES. *C. lacustris* Gervais 1856; *C. minor* Gervais 1876 (including *C. helveticus* (Pictet & Humbert 1869) Sudre 1978*b*); *C. ruetimeyeri* Stehlin 1908; *C. robiacensis* Depéret 1917; *C. fontensis* Sudre 1978*b*; and *C.* aff. *fontensis*.

RANGE. Late Lutetian–late Ludian; England, France, Switzerland and Spain.

EMENDED DIAGNOSIS. $\mathrm{P}\frac{1}{1}$ large and caniniform; C_1 incisiform. Upper cheek teeth with strong mesial and distal cingula and crests. Upper molars with: large paraconule; lingual crown height $\geqslant$ buccal crown height; fused lingual roots; postprotocrista restricted to distal wall of protocone; protolophule which may or may not join paracone. P^4 protocone lingual to paracone. P^3 protocone lingual or distolingual to paracone; P^3 outline may or may not narrow mesially. P^2 protocone present or absent. Lower molars with angles of protoconid and hypoconid crests acute. Supraorbital foramina above level of M^2 or M^3. Adult horizontal mandibular ramus about twice as deep below M_3 as below P_2.

SIGNIFICANCE OF THE SUBGENUS *Gervachoerus*. Sudre (1978*b*: 56–57) erected his new subgenus with *C. minor* as its type species. The characters which he used, however, were based on a referred cranium and mandible from Euzet (figured by Depéret 1917: pl. 17, figs 4–6). Contrary to his diagnosis of *Gervachoerus*, the holotype maxilla of *C. minor* (MNHN Qu60b) has upper molars with central accessory conules, and a topotype maxilla (MNHN Qu71) has P^3 roots indicating a longer, narrower tooth than P^4 and which is broader distally than mesially. Material from Lamandine (the type locality) is not complete enough to comment on the other characters listed for *Gervachoerus*, but the only species known to have the mandible shallow



Text-figure 56 Disto-occlusal views of upper preultimate molars of *Cebochoerus* and *Acotherulum*, about ×4. A, left M^2 of *C. fontensis* Sudre (UM F4-214) from Fons 4; B, left M^2 of *C.* aff. *fontensis* (UL 6145) from Euzet; C, right M^2 (reversed) of *C. robiacensis* Depéret (M7528) from Caylux; D, right M^1 (reversed) of *A. quercyi* (Stehlin) (MNHN Qu7075) from Bach; E, left M^1 of *C.* '*helveticus*' (Pictet & Humbert) (LGM LM808) from Mormont; F, left M^1 of *C. minor* Gervais (MNHN Qu11283) from Lamandine. A, B, D, E and F are drawn from casts.

from front to back is '*G.*' *campichii*, here shown to belong to *Acotherulum* (see p. 399). The presence on the upper molars from Lamandine of a protolophule joining the paracone and almost equal buccal and lingual crown height indicates close relationships with *C. lacustris* and *C. helveticus* (which Sudre referred to the nominate subgenus) rather than to the Euzet skull or to other species Sudre placed in *Gervachoerus*, such as *G. fontensis* (see Text-fig. 56).

It is concluded that: 1, *Gervachoerus*, based as it must be on *C. minor*, is not sufficiently distinct from the nominate subgenus, based on *C. lacustris*, to warrant subgeneric separation; 2, Sudre's concept of *Gervachoerus* is almost entirely a phylogenetic one which includes species attributable on characters to both *Cebochoerus* and *Acotherulum*; and 3, the Euzet material cannot belong to *C. minor* and requires a new specific name, if it is not conspecific with *C. fontensis* (it is referred to here as *C.* aff. *fontensis*).

Cebochoerus minor Gervais 1876
(Pl. 31, fig. 1; Text-figs 57, 58B, 59, 60A)

v. *1972* *Cebochoerus* sp.; Hooker: 180–181.
v? *1977b* Creodonta or Carnivora indet.; Hooker: 141.
v. 1978*b* *Cebochoerus helveticus* (Pictet & Humbert)?; Sudre: 72, 74.
v. *1980* *Cebochoerus* sp. 1; Hooker & Insole: 44.

HOLOTYPE. Left maxilla with M^{1-3} (MNHN Qu60b). Early Ludian limestone; Lamandine, Quercy, France (see Pl. 31, fig. 2). This specimen was to have been figured by Gervais (1876: pl. XI, figs 7–8), but his plate XI appears never to have been published.

RANGE OF SPECIES. Marinesian, England; early Ludian, France and Spain; probably Marinesian, Switzerland and France.

MATERIAL. Slightly crushed cranium in three pieces, lacking braincase, and with crowns of left P^3–M^3 and right P^4–M^1; roots of left and right C^1–P^1 and left P^2; and alveoli of right I^{2-3} (M26649).

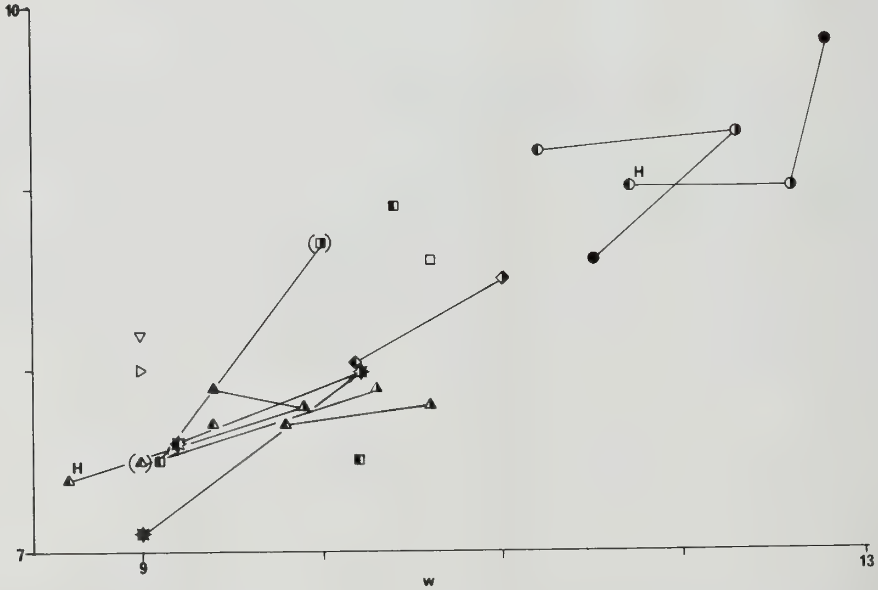
HORIZON AND LOCALITY. Bed C (0·6 m (= 2 ft) below top nodule band), Barton Clay Formation, Barton Cliff, east of Chewton Bunny, Hampshire. In wavewashed lower part of cliff at about SZ 226930. Collected by Mr & Mrs P. Clasby.

DOUBTFULLY REFERRED MATERIAL. Five mainly poorly-preserved anterior permanent and/or deciduous lower premolars (M36199, M36403, M36801, M37551, M37565) from the Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS. Medium-sized *Cebochoerus* (mean length of M^1 = 7·5 mm; see Text-fig. 57). Upper molars with: protolophule joining paracone; and lingual crown height = buccal crown height. P^4 width/length ratio 1·4. P^3 with protocone distolingual to paracone; and outline narrowing mesially. [Crown of P^2 unknown]. Supraorbital foramina above level of M^3. Frontals not extended posteriorly from postorbital processes.

DESCRIPTION OF CRANIUM. The specimen is very fragile and after being cleaned of matrix was filled with carbowax to give it support. Slight crushing has bent the ventral part of the left maxilla, posterior to the infraorbital foramen, plus the jugal, the ventral half of the lacrymal and the palate in a medial direction, so that in ventral view the teeth anterior to left P^3 appear to splay laterally. The left nasal and frontal have detached from the maxilla at the intervening sutures and slid beneath it slightly. The result in dorsal view is that the midline suture has come to lie nearer to the left than the right maxilla.

Incisors. The right premaxilla has a complete circular alveolus for I^3. It is about 20° from the vertical and not separated from the canine by a diastema. Parts of the I^2 alveolus are present,



Text-figure 57 Scatter diagram of length (l) against width (w) in upper molars of the *Cebochoerus minor/helveticus/lacustris* complex. ○ = *C. lacustris* Gervais from Souvignargues (H = holotype) and Mémerlein; □ = *C. 'helveticus'* (Pictet & Humbert) from Mormont; △ = *C. minor* Gervais from Lamandine; ▽ = *C. minor* from Sosis; ▷ = *C. minor* from Le Bretou; ◇ = *C. minor* from Fons 6; ☆ = *C. minor* from Barton. Symbols solid on left = M^1, solid on right = M^2; completely solid = M^3; outline = $M^{1/2}$. Measurements in millimetres. Lines join teeth of one individual.

anteromedial to I^3 and orientated at about 45° to the vertical. There is no evidence for an I^1 but there would be room for it between I^2 and the midline. In the Mémerlein cranium of *C. lacustris*, the premaxilla appears blunter anteriorly than that of M26649 with the incisor alveoli more transversely orientated. There may, however, be some distortion in the Mémerlein specimen, hidden beneath a crust of matrix. No other known cebochoerid crania have this region preserved.

Canines. These are two-rooted and only slightly smaller than the right canine of *C. lacustris* (proportional with the cheek teeth). The upper canine of the Euzet *C.* aff. *fontensis* cranium appears both proportionally and absolutely smaller.

Premolars. Like the canines, the P^1s are two-rooted and absolutely but not proportionally slightly smaller than those of *C. lacustris*, but are both absolutely and proportionally larger than those of *C.* aff. *fontensis*. They are separated from both canines and P^2s by short diastemata as in these other two species.

The two roots of P^2 have been damaged by the axis of diagenetic bending of the cranium.

P^3 is long, narrow and wedge-shaped with a small distolingual protocone, which makes the tooth wider distally then mesially. The roots on a topotype of *C. minor* (MNHN Qu71; Pl. 31, fig. 3) suggest a similar crown morphology. Both are certainly very different from *C.* aff. *fontensis* whose P^3 has a large lingual protocone. *C. lacustris* from Mémerlein and *C.* '*helveticus*' (Stehlin 1908: pl. 14, fig. 17) have a P^3 protocone larger than that of the Barton specimen, but like the latter and unlike *C.* aff. *fontensis* it is distolingual in position. In the Barton specimen there is a small metacone midway along the postparacrista, as in *C. lacustris* and *C.* '*helveticus*' and unlike *C.* aff. *fontensis*.

The P^4s are transverse and triangular, with pre- and post-cingula which do not meet round the protocone. There is a distal accessory conule, more distinct on the right than on the left tooth. *C.* '*helveticus*' (NMB Mt2) has a very similar P^4. On the Mémerlein *C. lacustris*, the pre- and post-cingula are stronger, the former bypassing the postprotocrista and fusing with the 'paracingulum'. *C.* aff. *fontensis* has a less transverse P^4 with short weak precingulum and no postcingulum and the protocone with its crests is higher.

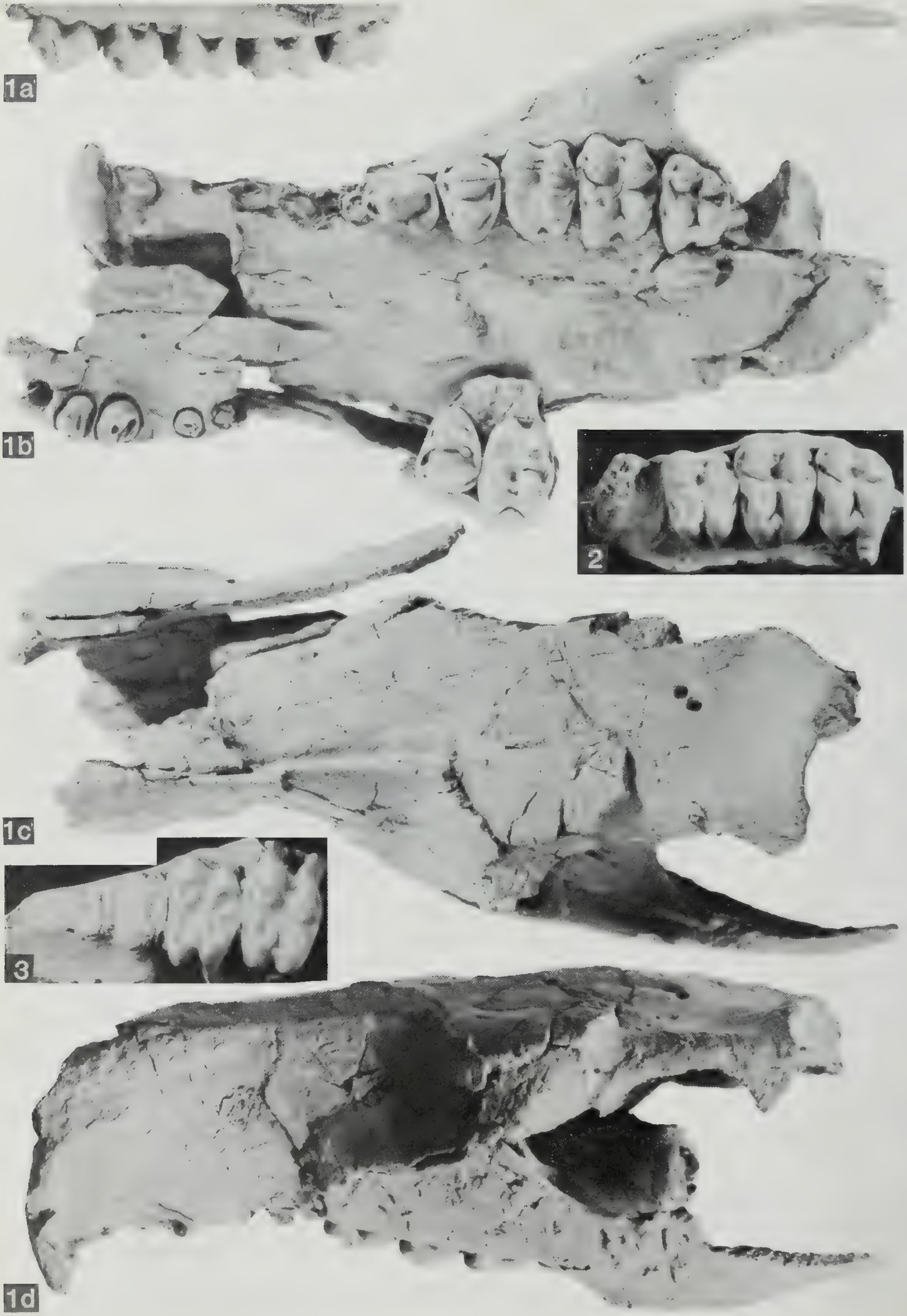
Molars. These resemble *C. minor*, *C. lacustris* and *C.* '*helveticus*' in the presence of a protolophule joining the paracone and in the premetaconule crista tending to form a prominent central accessory conule and to join the metacone. Buccal cingula are restricted to between the paracone and metacone and near the parastyle and metastyle. There is a very small mesostyle on M^2 and a larger one on M^3 associated with buccal flexing of the centrocrista. These cingular features show much variation in *C. minor* from Lamandine, three specimens including the holotype having a strong cingulum round the metacone, one having a complete buccal cingulum and two others being like the Barton specimen. The fact that the Mémerlein *C. lacustris* upper molars have the buccal cingulum continuous round the metacone is thus not considered a taxonomic difference either from the Barton specimen or from specimens of *C. minor* from the type locality. Similar variation occurs in *C.* '*helveticus*' but no specimens appear to exist with a complete buccal cingulum.

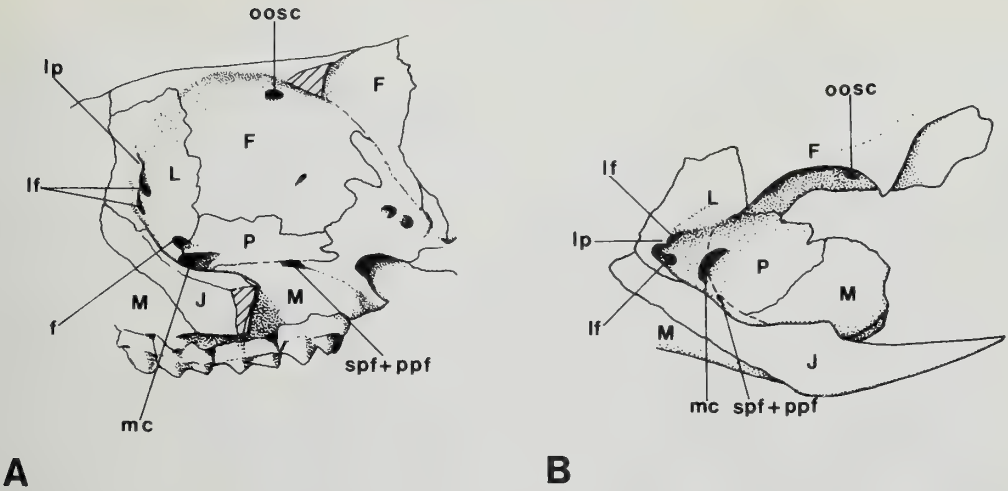
Osteology. The cranium is smaller than, but otherwise very similar to, that of *C. lacustris* from Mémerlein, which has been extensively described and figured by Pearson (1927). Only those features which are new or differ from this species are described here.

Recognition of sutures and orbital foramina is made difficult by surface erosion and crushing. Text-figs 58–59 attempt to show these and other features and reconstruct the cranial shape. I have relied heavily on the well-preserved cranium of *A. saturninum* (MNHN Qu16366, holotype of *Leptacotherulum cadurcense*) to guide interpretation of sutures and foramina (Text-fig. 58A; see also Russell 1964: 263, text-fig. 57).

The left frontal preserves twinned supraorbital foramina, probably an individual character (cf. Sisson & Grossman 1953: 137, for *Bos taurus* L.). Their position above M^3 is like *C. lacustris* (see Pearson 1927). In the crania of all other species of *Cebochoerus* and *Acotherulum*, where this feature is known, they are above M^2 (viz. *C.* aff. *fontensis*, *C. robiacensis*, *A. saturninum* and *A. quercyi*).

Immediately behind the postorbital process the anterior (frontal) edge of the temporal fossa


1a
1b
2
1c
3
1d



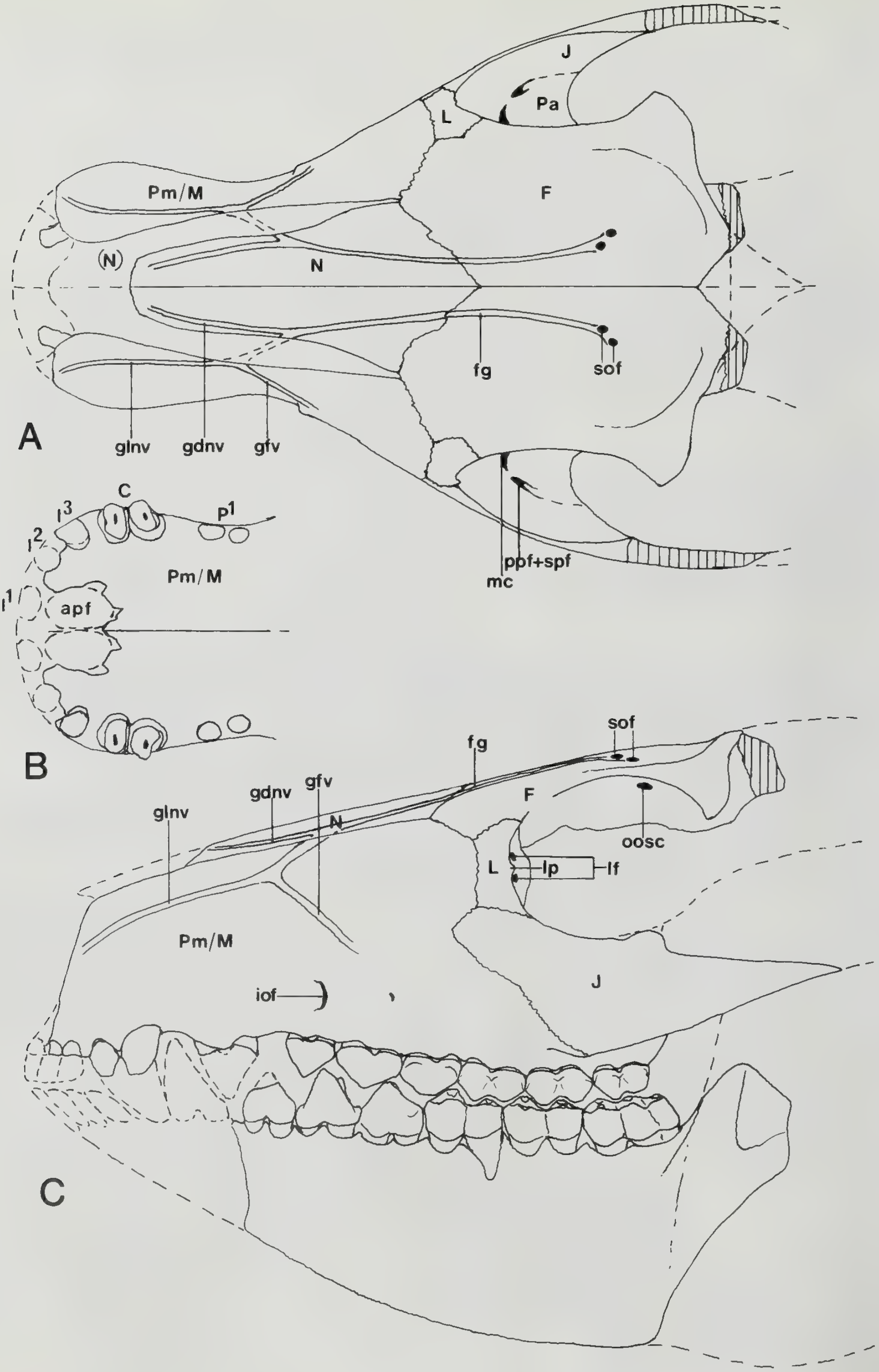
Text-figure 58 Left orbital regions of A, *Acotherulum saturninum* Gervais (holotype of *Leptacotherulum cadurcense* Filhol) from the Phosphorites du Quercy (MNHN Qu16366) (right side reversed); and B, *Cebochoerus minor* Gervais from Bed C, Barton Clay, Barton Cliff (M26649). Both × 1·3. Abbreviations: F = frontal; f = fossa (?for origin of the ventral oblique muscle of eyeball); J = jugal; L = lacrymal; lf = lacrymal foramen; lp = lacrymal process; M = maxilla; mc = maxillary canal; oosc = orbital opening of supraorbital canal; P = palatine; ppf = postpalatine foramen; spf = sphenopalatine foramen.

has a transverse orientation. This is like all cranially known *Acotherulum* and *Cebochoerus* species except *C. lacustris*, where the frontal extends backwards from the postorbital process almost to a position vertically above the anterior edge of the squamosal (see Pearson 1927: text-fig. 22).

The anterior edge of the very shallow narial incision is preserved on the right premaxilla and on a tiny fragment of the right nasal. The configuration is very similar to that of *C. lacustris*, the only other cebochoerid where this part is known. The maxillary–premaxillary suture is not visible, apparently owing to fusion of these bones. Part of the edge of the right anterior palatine foramen is preserved, a feature covered by matrix/plaster on the *C. lacustris* cranium and unknown in any other specimen.

SIGNIFICANCE OF THE P^3 CHARACTERS IN *C. minor*. The difference in protocone size between *C. minor* on the one hand and *C. 'helveticus'* and *C. lacustris* on the other is not taken here to be a specific character because of variation in the relevant occluding parts of P_4s of *C. minor*: in particular two jaws with lightly worn premolars, one from Lamandine (MNHN Qu67) and another with no detailed provenance but of very similar preservation (MNHN Qu79). In Qu79 the P_4 paracristid has a doubly concave buccal phase facet which would have occluded with a P^3 postparacrista with small metacone. A lingual phase facet is present near the tip of the protoconid, sloping mesiolingually at a shallow angle; this would have made contact with a small distolingual P^3 protocone such as occurs on the Barton cranium. Qu67 (Filhol 1877*b*: pl. 14, figs 288–290) has a similar but more worn and flatter buccal phase facet on the P_4

Plate 31 Light macrographs of *Cebochoerus minor* Gervais, × 1·6. Fig. 1a–d, partial cranium (M26649) from Barton Cliff; in lateral (a, left cheek tooth row only), ventral (b), dorsal (c) and left dorsolateral (d) views. Fig. 2, holotype left M^{1-3} (MNHN Qu60b) from Lamandine, in occlusal view. Fig. 3, right M^{1-2} with roots of P^{3-4} (reversed) (MNHN Qu71) from Lamandine, in occlusal view. See p. 391.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paracristid and another buccal phase facet near the tip of the large metaconid caused by contact with the postprotocrista of a P^3. Also on the paracristid but lingual to the buccal phase facet is a long lingual phase facet sloping steeply in a mesial direction. This would have been caused by a larger, less distal P^3 protocone. Whether this protocone would resemble that of *C. lacustris* or *C.* aff. *fontensis* remains unclear, but P^3 and P_{3-4} appear to be rather variable teeth in *C. minor*. Similar potential variation is demonstrated by two Mémerlein mandibles, one belonging to the cranium and an immature one consisting mainly of symphysis (M32172) with an unerupted P_3. In the latter, P_3 has a prominent metaconid distolingual to the protoconid, whereas in the former the metaconid is smaller and distal to the protoconid.

DISTINGUISHING FEATURES OF *C. minor*, *C. 'helveticus'* AND *C. lacustris*. The only observable difference between *C. minor* and *C. lacustris*, apart from size, is in the anterior edge of the temporal fossa. *C. 'helveticus'* is intermediate in size between the two, no cranial characters are known and it resembles *C. lacustris* in its partly unreliable P^3.

Sudre's (1978*b*: 75–76) diagnosis and discussion of *C. lacustris* does not help as it is mainly concerned with distinguishing it from '*G.*' *minor*, not *C. helveticus*. Recorded contemporaneity of *C. minor* and *C. lacustris* applies to the type locality of the former (Lamandine) and relies on Stehlin's (1908: 742) determination of specimens in Montauban and Munich museums. The quoted measurements indeed compare well with those of the Mémerlein skull of *C. lacustris*. The measurements which Sudre (1978*b*: 75) quoted for the now lost holotype maxilla of *C. lacustris* (8 mm for each of the three molars) are taken from Gervais' (1876: 48) type description of *C. minor*, not *C. lacustris*. Therefore his maxilla from Fons 6 and the tooth from Sosis can reasonably be reidentified as *C. minor*. Gervais (1859: 197–198, text-fig. 20), in the first meaningful description of the holotype of *C. lacustris*, gave M^{1-3} length as 27 mm, width of M^1 as 21 mm (which must be an error) and P^3–M^3 length as 41 mm.

Text-fig. 57, p. 392, shows length and width of upper molars for these three species. It shows the Barton cranium to plot easily within the range of variation of the type assemblage of *C. minor*. The known specimens of *C. 'helveticus'* (type assemblage only) overlap with *C. minor* and approach *C. lacustris*. There are several possible conclusions on the status of *C. 'helveticus'* from these data: 1, it consists of a mixed assemblage of *C. minor* and *C. lacustris*; 2, it is a species distinct from either, differing in characters as yet unknown; or 3, it is conspecific with *C. minor*, representing a degreee of intraspecific variation resulting from geographical and/or stratigraphical differences. Text-fig. 60A is a cumulative graph of coefficients of variation for the measurements given in Text-fig. 57. A variable but low v for seven *C. minor* specimens from Lamandine is increased to 6·4 in length and 7·7 in width when *C. 'helveticus'* measurements are added. These coefficients are still insufficient to demonstrate a specific separation of *C. 'helveticus'* from *C. minor*. They support the choice of conclusion 3 above, although conclusion 2 can never be excluded. The addition of measurements of specimens from Sosis, Le Bretou, Fons 6 and Barton reduces the coefficient, but the addition of two specimens of *C. lacustris* raises it to a level which suggests that on size alone more than one species is now represented.

It is possible that speciation resulted from isolation during the Bartonian. Perhaps the Swiss and French assemblages gave rise to *C. lacustris* by slight size increase; English *C. minor* remained unchanged but spread to France and Spain after the end of the Bartonian.

Text-figure 59 Partial reconstruction of skull of *Cebochoerus minor* Gervais. Cranium based on M26649 from Bed C, Barton Clay, Barton Cliff; mandible on MNHN Qu67 from Lamandine. × 1·3. Abbreviations: apf = anterior palatine foramen; F = frontal; fg = frontal groove; gdnv = groove for dorsal nasal vein; gfv = groove for facial vein; glnv = groove for lateral nasal vein; iof = infraorbital foramen; J = jugal; L = lacrymal; lf = lacrymal foramen; lp = lacrymal process; M = maxilla; mc = maxillary canal; N = nasal; oosc = orbital opening of supraorbital canal; Pa = palatine; Pm = premaxilla; ppf = postpalatine foramen; sof = supraorbital foramina; spf = sphenopalatine foramen. A, dorsal view of cranium, B, ventral view of anterior end of palate and C, left lateral view of cranium and mandible.

Cebochoerus robiacensis Depéret 1917
(Pl. 32, figs 2, 4, 5; Text-fig. 60B)

v. *1977b* *Cebochoerus* cf. *ruetimeyeri* Stehlin; Hooker: 141.
v. *1980* *Cebochoerus* cf. *ruetimeyeri* Stehlin; Hooker & Insole: 44.

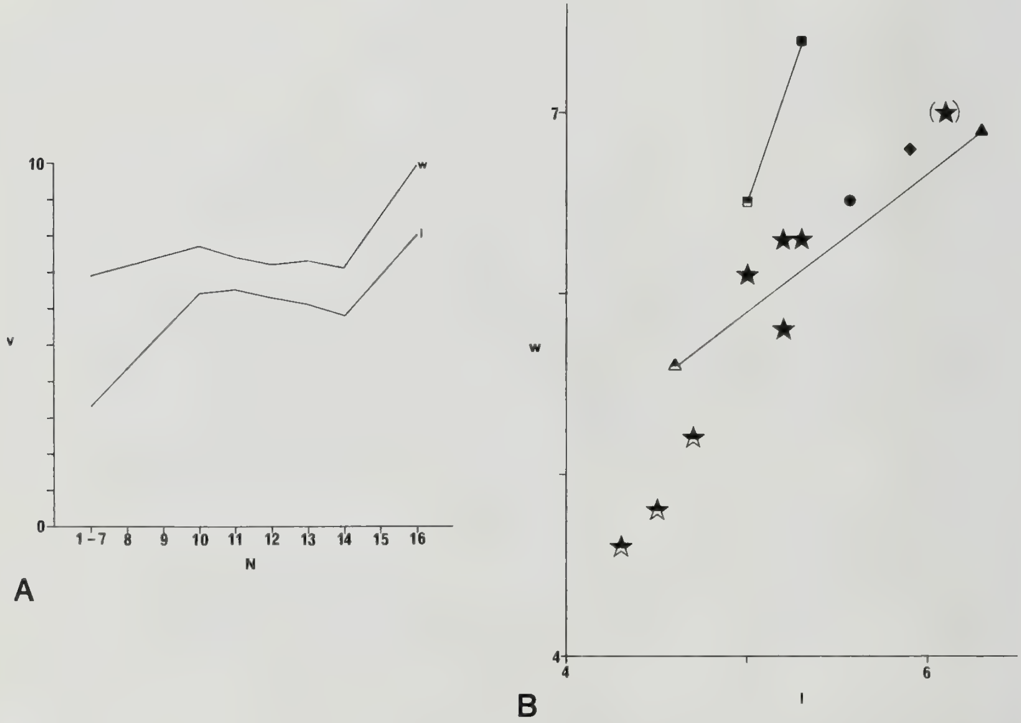
LECTOTYPE. Right maxillary fragment with M^{2-3} (NMB Rb52). Marinesian, Robiac (figured Stehlin 1908: text-fig. 109); selected Sudre, 1969*a*: 125.

RANGE. Marinesian, England and France.

MATERIAL. Right M^3 (M36803); right DP^4 (M37498); left $M_{1/2}$ (M37501); 2 right $M_{1/2}$ trigonid fragments (M36860, M37504); and possibly a distal fragment of left DP_4 (M37503).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Small *Cebochoerus* (mean length of M^1 = 5·3 mm). Upper molars with: protolophule not joining paracone; and lingual crown height > buccal crown height. P^4 width/length ratio 1·1. P^3 with protocone lingual to paracone; and outline not narrowing mesially. P^2 with protocone. Supraorbital foramina above level of M^2. Frontals not extended posteriorly from postorbital processes.



Text-figure 60 A, cumulative curves of coefficients of variation for lengths and widths of M^1 of the *Cebochoerus minor/helveticus/lacustris* complex. 1–7 from Lamandine; 8–10 from Mormont; 11 from Sosis; 12 from Le Bretou; 13 from Fons 6; 14 from Barton; 15–16 from Souvignargues and Mémerlein. B, scatter diagram of length (l) against width (w) in P^4 and M^3 of *Cebochoerus robiacensis* Depéret and *Acotherulum campichii* (Pictet). △ = *C. robiacensis* from Lautrec (measured from cast); ◇ = *C. robiacensis* from Caylux; ○ = *C. robiacensis* from Robiac; □ = *A. campichii* from Mormont (measured from Stehlin 1908: pl. 14, fig. 6); ☆ = *C. robiacensis* and *A. campichii* from Creechbarrow. Symbols solid above = P^4; completely solid = M^3. Measurements in millimetres. Lines join teeth of one individual.

Description and discussion. Sudre (1978*b*: 66) synonymized this species with *Acotherulum campichii* (Pictet) comb. nov. (p. 400), which he referred to the genus *Cebochoerus*. In discussing his identification of specimens as '*C.*' *campichii*, he noted that the maxilla from Mormont figured by Stehlin (1908: pl. 14, fig. 6) differed from the Robiac material in having broader P^4 and shorter M^3. He considered that these characters had no evolutionary value and constituted simply individual variation. Three more characters – small upper molar paraconule, mesiolingual P^4 protocone and weak mesial and distal cheek tooth cingula and crests – also distinguish the Mormont maxilla from the Robiac material. These last characters are constant for three P^{4}s and five upper molars from Creechbarrow. These specimens are thus referred to *A. campichii* (see p. 400) and demonstrate the taxonomic importance of these characters in the distinction of *C. robiacensis* from *A. campichii.*

The Creechbarrow M^3 (M36803, Pl. 32, fig. 4) can be distinguished further from those of *A. campichii* by being slightly larger and by the mesial margin being convex, because of the bulging paraconule. Its paracone is broken buccally but a buccal cingulum appears to have continued round this cusp from the metaconal region. The cingula of the lectotype, according to Stehlin's figure, have a similar extent; but further specimens from Robiac, Lautrec (Sudre 1978*b*: text-pl. 6, figs 1, 3) and Caylux (Pl. 32, fig. 8) have weaker buccal cingula, showing this to be a variable feature.

The DP^4 (Pl. 32, fig. 2) has thinner enamel than the M^3; an almost complete strong buccal cingulum, only slightly interrupted at the paracone; shallow concave valleys; and a strong postprotocrista which almost joins the premetaconule crista.

The lower molars can be distinguished from those of *A. campichii* by having the mesial and distal crests of protoconid and hypoconid meeting at acute angles. M37501 has a mesoconid but this is a variable feature, common in *Cebochoerus*, less common in *Acotherulum*. It also has the hypoconulid at a more longitudinal orientation to the postcristid; this is another feature which is variable but more common in *Cebochoerus* than *Acotherulum* (see Pl. 32, figs 5b, 6b). The character of the hypoconulid is also visible on the DP$_4$ fragment.

C. robiacensis has not previously been given a character diagnosis. Authors have tended only to seek recognition of it either as the ancestor of *C. minor* (Depéret 1917: 113) or the descendant of '*C.*' *suillus* (Stehlin 1908: 745). Although relatively easily distinguishable from *A. campichii*, as shown above, it is less easily separated from the Auversian *C. ruetimeyeri*. *C. ruetimeyeri* is usually slightly larger and tends to have stronger buccal and lingual cingular developments, but there is much overlap. The most reliable difference appears to be lower lingual crown height of upper molars in *C. ruetimeyeri*, this being approximately equal to the buccal crown height.

Genus *ACOTHERULUM* Gervais 1850

[incl. *Metadichobune* and *Leptacotherulum* Filhol 1877*a*, *Cebochoerus* (*Gervachoerus*) Sudre 1978*b* in part, and ?*Moiachoerus* Golpe-Posse 1972]

Type species. *A. saturninum* Gervais 1850. Ludian; La Débruge, Vaucluse, France (?including *Leptacotherulum cadurcense* Filhol 1877*a*).

Included species. *A. quercyi* (Stehlin 1908) Sudre 1978*b*; *A. campichii* (Pictet 1857) comb. nov.; *A. pumilum* (Stehlin 1908) Sudre 1978*b*; *A.* sp. (Bembridge Limestone).

Range. Marinesian to late Ludian, England; Marinesian to Ludian, France and Switzerland; Ludian, Spain; and early Stampian, Belgium.

Emended diagnosis. P$\frac{1}{1}$ large and caniniform; C$_1$ incisiform. Upper cheek teeth with weak mesial and distal cingula and crests. Upper molars with: small paraconule; lingual crown height > buccal crown height; fused or unfused lingual roots; postprotocrista restricted to distal wall of protocone; protolophule not joining paracone. P^4 protocone mesiolingual to paracone. P^3 protocone lingual to paracone; P^3 outline narrowing mesially. P^2 protocone absent. Lower molars with angles of protoconid and hypoconid crests right-angled to obtuse. Supraorbital foramina above level of M^2. Adult horizontal mandibular ramus scarcely deeper below M$_3$ than below P$_2$.

Acotherulum campichii (Pictet 1857) comb. nov.
(Pl. 32, figs 1, 3, 6, 7; Text-fig. 60B)

v. *1977b* *Cebochoerus* cf. *campichii* (Pictet) Stehlin; Hooker: 141.
v. *1980* *Cebochoerus* cf. *campichii* (Pictet) Stehlin; Hooker & Insole: 44.

HOLOTYPE. Right mandibular ramus with P_1–M_2. Sidérolithique; Mormont, Canton Vaud, Switzerland (figured Pictet 1857: pl. 4, figs 5–9), now lost according to Stehlin (1908: 729). De la Harpe (1869: 466) recorded the species (as *Dichobune Campichii*) from only one of the Mormont localities – Gare d'Eclépens, so it can be concluded that the missing holotype came from there.

RANGE. Marinesian; England, France and Switzerland.

MATERIAL. Three right P^4s (M36191, M36807, M37497); two left M^3s (M36802, M37499); two right M^3s (M36804, M37500); mesial fragment of right upper molar (M36805); left $M_{1/2}$ (M37502); and left M_3 lacking trigonid (M36183).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS. Medium–small *Acotherulum* (length of M^1 = 5·6 mm). Upper molar lingual roots fused. $M_{1/2}$ more than half as wide as long.

DESCRIPTION. Size appears to be slightly less than in the Mormont material (see Text-fig. 60B and Stehlin 1908: 731; pl. 14, fig. 6).

P^4: M37497 is very worn and shows few detailed features. M36191 shows a small metacone immediately behind the paracone. M36807 has no metacone. Both M36191 and M37497 have suggestions of a distal accessory conule and M37497 also a paraconule. In M37497, distinction from *C. robiacensis* can still be made by the position of the protocone and the low mesial and distal crests and cingula which have hardly been affected by the heavy wear which has removed most of the paracone and protocone (cf. Sudre 1978*b*: text-pl. 6, figs 1b, 3).

M^3: Variation is mainly in outline shape and distribution of cingula. The terminal bulge of the outline is midway along the metacingulum in M37499 and M36804 and is in the metastylar region in M36802 and M37500. The cingulum is continuous round the metacone in M37499, M36804 and M36802. In M37500, the precingulum does not extend as far lingually as in the other three. M36804 is the only specimen with even the slightest development of a postcingulum. M36802 and M36804 each have a very small accessory conule. This is absent in M37500 and the area is too worn to tell in M37499. All have small paraconules, which distinguish them from *C. robiacensis* from the same locality (see p. 398).

$M_{1/2}$: M37502 is significantly narrower relatively than the same tooth attributed herein to *C. robiacensis*; it has no mesoconid; the paracristid is bent asymmetrically; the hypoconulid merges gradually with the postcristid; and the tooth as a whole appears less robust.

M_3: What remains of M36183 is fairly worn. It appears to have been relatively narrow; there is a lingual accessory conule between the entoconid and hypoconulid; and the cingula are weak. Size and the accessory conule are more consistent with attribution to *A. campichii* than to *C. robiacensis*.

PHYLOGENETIC IMPLICATIONS WITHIN THE CEBOCHOERIDAE. Table 34 compares characters of the various species of *Cebochoerus* and *Acotherulum*. Primitive versus advanced states have been

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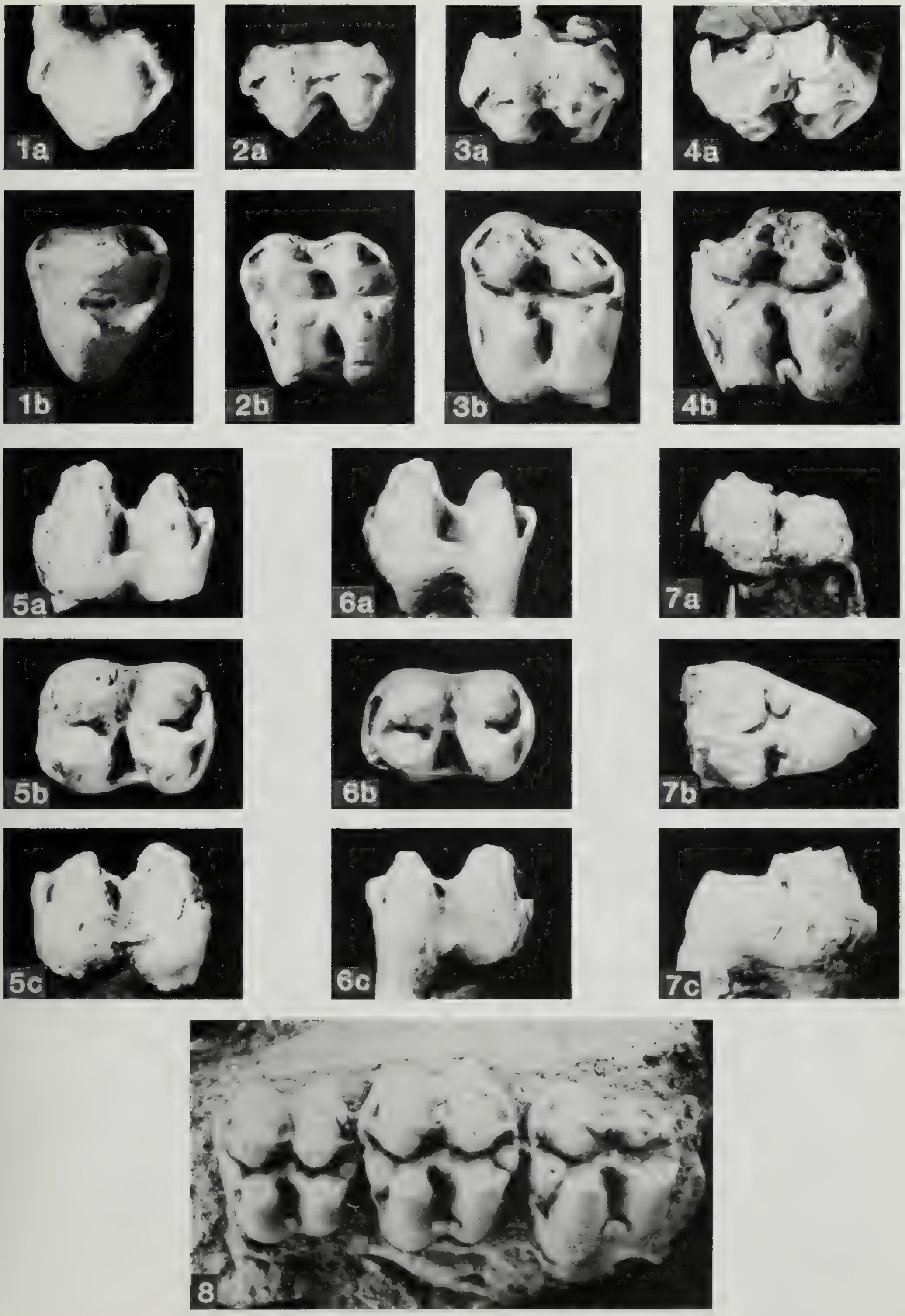
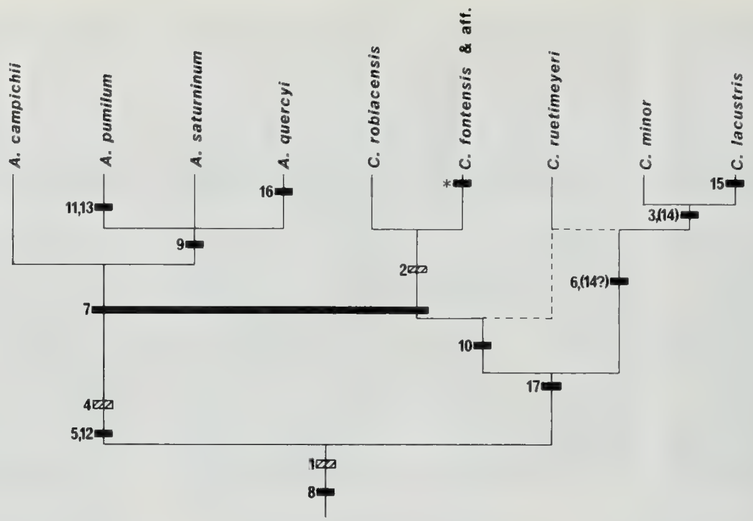
Plate 32 Light macrographs of cheek teeth of *Cebochoerus* and *Acotherulum*, × 5. Views are buccal (a), occlusal (b or unsuffixed) and lingual (c).

Figs 1, 3, 6, 7 *Acotherulum campichii* (Pictet) from Creechbarrow. Fig. 1a, b, right P^4 (reversed) (M36807). Fig. 3a, b, right M^3 (reversed) (M37500). Fig. 6a–c, left $M_{1/2}$ (M37502). Fig. 7a–c, left M_3 talonid fragment (M36183). See above.

Figs 2, 4, 5 *Cebochoerus robiacensis* Depéret from Creechbarrow. Fig. 2a, b, right DP^4 (reversed) (M37498). Fig. 4a, b, right M^3 (reversed) (M36803). Fig. 5a–c, left $M_{1/2}$ (M37501). See p. 398.

Fig. 8 *Cebochoerus robiacensis* Depéret from Caylux. Right maxilla with M^{1-3} (reversed) (M7528).


1a
2a
3a
4a
1b
2b
3b
4b
5a
6a
7a
5b
6b
7b
5c
6c
7c
8



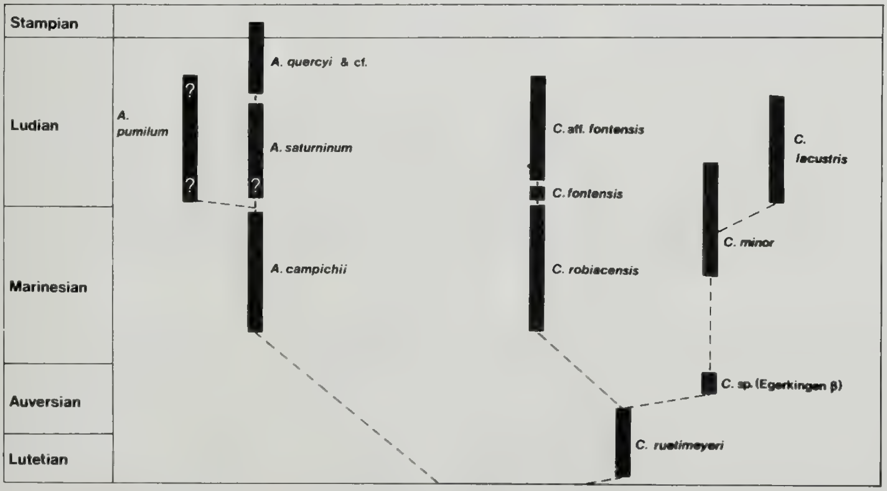
Text-figure 61 Cladogram of species of *Acotherulum* and *Cebochoerus*. This is the most parsimonious possibility. Character 7 is apparently the only parallelism. Because of the incompleteness of certain species, some of their character states are unknown (see Table 34 opposite). Two of these characters (15 and 16) are each only known in a single species, unknown in closely related species and define terminal dichotomies. Their occurrence in the poorly-known, less related forms is unlikely, but if shown to occur they would be incongruent with other characters and would thus be parallelisms. Most of the other incompletely known characters are more fundamental and are shown hatched. Character 2 is poorly known in *Acotherulum* but is tentatively considered consistently primitive, as in its advanced state it is distinctive of only two species of *Cebochoerus*. The problems posed by characters 1, 3 and 4 could be overcome by excluding the very poorly known *A. pumilum* from the cladogram. *C. ruetimeyeri* is variable for two characters which are constant but different in the two terminal groups of *Cebochoerus*. Using only the advanced states of these characters, *C. ruetimeyeri* can be related equally to the *C. robiacensis/fontensis* group or to the *C. minor/lacustris* group, unless in the future it is found to have the advanced state for character 14. This would relate it more to the latter group, but it remains otherwise totally primitive within the genus *Cebochoerus*. Lack of knowledge of certain characters renders the cladogram very tentative, but it may be hoped the gaps will be filled by the anterior dentition and skull parts eventually becoming known for the incomplete species. By applying the cladogram to the occurrence of the species in the stratigraphical record, the phylogeny shown in Text-fig. 62 is produced. (* = greater size.)

calculated by outgroup comparison with the rest of the Dichobunoidea, except character 14, which was by ingroup comparison as it is relatively poorly known outside the Cebochoeridae. *C. suillus* (Gervais 1852) Stehlin 1908, *C. dawsoni* Sudre 1978*b* and *C. jaegeri* Sudre 1978*b* are omitted since distinctive characters such as small premolariform P_1 and upper molar post-protocrista joining metaconule indicate that a new genus is required to include them.

One way of displaying these character distributions is in the form of a cladogram (Text-fig. 61). *Cebochoerus ruetimeyeri* shares incipient development of advanced character 10 with the *C. robiacensis/fontensis* group and of advanced character 6 with the *C. minor/lacustris* group. It is otherwise primitive with respect to both, which makes *C. ruetimeyeri* from Egerkingen α a good candidate for their common ancestry. These groups correspond partially to Sudre's subgenera *Gervachoerus* and *Cebochoerus* respectively, but are much more restricted. A maxilla from Egerkingen β was referred to *C. ruetimeyeri* by Stehlin (1908: pl. 14, fig. 55). It is intermediate between the latter and *C. minor* in size and has an upper molar protolophule joining the paracone, as in *C. minor*. A phylogeny is proposed in Text-fig. 62.

Table 34 Characters and character states of species in the genera *Cebochoerus* and *Acotherulum*. Characters are estimated as primitive (–) or advanced (+) based on outgroup comparison with the rest of the Dichobunoidea. Lack of information on a character indicated by '?'.

Character	State		*A. campichii*	*A. saturninum*	*A. quercyi*	*A. pumilum*	*C. fontensis* & aff.	*C. robiacensis*	*C. ruetimeyeri*	*C. minor*	*C. lacustris*
	Primitive	Advanced									
1. $P\frac{1}{1}$ caniniform	no	yes	+	+	+	?+	+	+	+	+	+
2. P^2 protocone	absent	present	?	?	–	?	+	+	–	–	–
3. P^3 protocone position regarding paracone	lingual	distolingual	–	–	–	?–	–	–	–	+	+
4. P^4 protocone position regarding paracone	lingual	mesiolingual	+	+	+	?+	–	–	–	–	–
5. Upper molar paraconule	large	small	+	+	+	+	–	–	–	–	–
6. Upper molar protolophule joining paracone	no	yes	–	–	–	–	–	–	+/–	+	+
7. Upper molar lingual: buccal crown height	=	>1	+	+	+	+	+	+	–	–	–
8. Upper molar postprotocrista separate from metaconule	no	yes	+	+	+	+	+	+	+	+	+
9. Upper molar lingual roots	fused	separate	–	+	+	+	–	–	–	–	–
10. M^1/P^4 size ratio	high	low	–	–	–	–	+	+	+/–	–	–
11. P_4 paraconid high	no	yes	–	–	–	+	–	–	–	–	–
12. Angle of lower molar protoconid and hypoconid crests	acute	obtuse	+	+	+	+	–	–	–	–	–
13. Lower cheek teeth	wide	narrow	–	–	–	+	–	–	–	–	–
14. Supraorbital foramina above M^2 or M^3	M^2	M^3	?	–	–	?	–	–	?	+	+
15. Frontal projects behind postorbital process	no	yes	?	–	–	?	–	–	?	–	+
16. Jugal	shallow	deep	?	–	+	?	–	–	?	–	–
17. Horizontal mandibular ramus	shallow	deep	–	–	–	?–	+	+	+	+	+


Stampian
Ludian
Marinesian
Auversian
Lutetian
A. pumilum
?
?
A. quercyi & cf.
A. saturninum
?
A. campichii
C. aff. fontensis
C. fontensis
C. robiacensis
C. minor
C. lacustris
C. sp. (Egerkingen β)
C. ruetimeyeri

Text-figure 62 Proposed phylogeny of *Acotherulum* and *Cebochoerus* in the Eocene of Europe; based on the cladogram of Text-fig. 61 and stratigraphical occurrence.

Suborder **ANCODONTA** Matthew 1929*b*

Superfamily **ANTHRACOTHERIOIDEA** Gill 1872

Note that the Choeropotamidae are included here, not in the Dichobunoidea. Their differences from the Cebochoeridae are fundamental and I follow Stehlin (1908) in considering the family close to *Haplobunodon.*

Family **HAPLOBUNODONTIDAE** Pilgrim 1941 (*sensu* Sudre 1978*b*)

TYPE GENUS. *Haplobunodon* Depéret 1908.

INCLUDED GENERA. *Rhagatherium* Pictet 1857; *Amphirhagatherium* Depéret 1908; *Lophiobunodon* Depéret 1908; *Anthracobunodon* Heller 1934; *Masillabune* Tobien 1980; ?*Thaumastognathus* Filhol 1890*a*.

RANGE. Early Lutetian to late Ludian, Europe.

DIAGNOSIS. See Sudre (1978*b*: 90).

Genus ***HAPLOBUNODON*** Depéret 1908

[The main early generic and specific synonymies are complex and are dealt with by Stehlin (1908: 752–765)]

TYPE SPECIES. *H. lydekkeri* Stehlin 1908. Lower Headon Beds; Hordle Cliff, Hampshire. Nomenclatural background is given by Stehlin (1908: 752–754).

INCLUDED SPECIES. *H. solodurense* Stehlin 1908; *H. muelleri* (Rütimeyer 1862) Stehlin 1908; ?*H. ruetimeyeri* (Pavlow 1900) Stehlin 1908; and *H. venatorum* sp. nov.

RANGE. Late Lutetian to Ludian, Switzerland; Marinesian to early Ludian, France and England.

EMENDED DIAGNOSIS. $P\frac{1}{1}$ present to absent. No diastema between P_2 and P_3. P^{3-4} with outline as an isosceles triangle and without metacone. Upper molars semibunodont with mesostyles less than half the height of the paracone; paraconule smaller than protocone and not separated from it by deep fissure; premetaconule crista short, often joined to protocone. M^3 distal edge straight. P_{3-4} without hypoconid. P_4 often with large paraconid. Lower preultimate molars with postcristid joining hypoconulid usually independently of entoconid. [The otic region has been described by Pearson (1927: 438–440) for *H. lydekkeri,* but for no other haplobunodontid].

DISCUSSION. From Pavlow's (1900: pl. 5, figs 6–7) figures (fig. 6 reproduced by Stehlin, 1908: 773, text-fig. 112), *H. ruetimeyeri*, with large mesostyle, large paraconule and strongly oblique buccal edge distal to the mesostyle, fits Sudre's (1978*b*: 94–99; pl. 4, figs 7–8; pl. 5, fig. 5) concept of *Anthracobunodon* better than *Haplobunodon.* It could even be conspecific with *A. louisi* Sudre 1978*b* from Grisolles. Moreover, from outline shape and cusp pattern, the teeth in Pavlow's fig. 6 are more likely to be DP^4–M^1 than M^{1-2}.

Haplobunodon venatorum sp. nov.

(Pl. 33, figs 1–5; Pl. 34, figs 1–4; Text-figs 63–64; Table 35)

v. *1977b* *Haplobunodon* sp.; Hooker: 141.
vp. *1980* *Haplobunodon* spp.; Hooker & Insole: 44.

NAME. Latin, 'of the hunters', in allusion to the remains of a Mediaeval hunting lodge on the summit of Creechbarrow.

HOLOTYPE. Right P_4, M37540. Pl. 34, fig. 2.

PARATYPES. Two right P^4s, one fragmentary (M37712, M37528); right M^{1-2} associated (M37529); two fragmentary $M^{1/2}$s (M37530, M37713); two left M^3s (M37531–2); right M^3 (M37533); three fragmentary upper molars (M37535–7); left P_4 (broken)–M_2 (broken) (M37716); right P_3 (M37539); right P_4 (M37541); right $M_{1/2}$ (M37542); fragment of right mandibular ramus with M_3 (M37544); three left M_3s, all lacking trigonid (M37545, M37714–5); and right lower molar fragment (M37543).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

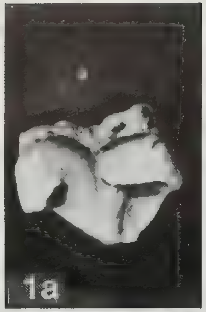
DIAGNOSIS. Large *Haplobunodon* (length of M^1 = 8·6 mm). P^4 broader than long, subtriangular in outline, with large protocone and strong ectocingulum and pre- and post-cingula. P_3 with metaconid and trifurcating postprotocristid. P_4 more than half as broad as long with metaconid and small entoconid present; and paraconid subequal in height to metaconid. Horizontal mandibular ramus not deepening beneath M_{1-3}.

DIFFERENTIAL DIAGNOSIS. *H. muelleri* is much smaller and has a mandibular ramus deepening from M_{1-3}; P_{3-4} are unknown. *H. lydekkeri* is slightly smaller; has a P^4 with an equilateral triangular outline, a smaller protocone, weaker ectocingulum and no pre- and post-cingula; a P_3 without metaconid and with single postprotocristid; and a P_4 with a large metaconid subequal with protoconid and a smaller paraconid. *H. solodurense* is slightly smaller, has a P_3 without a metaconid and a narrower P_4 with a paraconid but no metaconid or entoconid.

Table 35 Length (l) and mesial (w_1) and distal (w_2) width measurements of *Haplobunodon venatorum* from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M37712	RP^4	7·4	8·5	
M37529	RM^1	8·6	(10·3)	
M37529	RM^2	9·3	11·8	
M37532	LM^3	9·6	–	
M37531	LM^3	9·5	12·4	
M37533	RM^3	9·5	11·4	
M37716	LP_4	–	5·7	
M37716	LM_1	8·5	6·2	6·3
M37716	LM_2	–	7·9	–
M37539	RP_3	–	3·8	
M37540	RP_4	8·1	5·4	
M37541	RP_4	8·3	5·2	
M37542	R$M_{1/2}$	8·5	6·1	6·6
M37544	RM_3	13·5	7·9	6·9
M37545	LM_3	–	–	6·2
M37714	LM_3	–	–	6·6
M37715	LM_3	–	–	7·2
M37543	R$M_{1/2/3}$	–	6·7	–

DESCRIPTION. P^4: M37712 is quite worn. The cingula are faintly papillate. The ectocingulum, though strong, is interrupted between the midpoint on the paracone and the extensively crested parastyle. A small area of exposed dentine on the postparacrista indicates the presence of a tiny metacone. Its presence or absence in this state is intraspecifically variable in *H. muelleri* (see Stehlin 1910*b*: pl. 17, figs 35, 37). There is a worn swelling midway along the distal cingulum, which may have once been a small metaconule. There is a separation between this point and the postprotocrista which stops short, joining neither distal cingulum nor postparacrista.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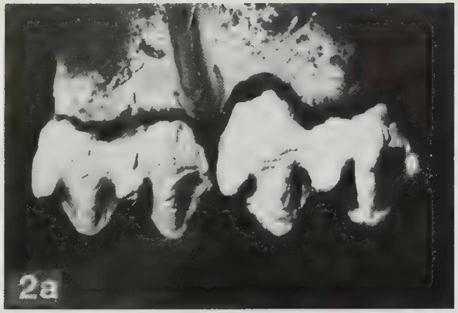
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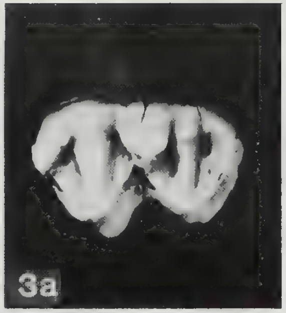
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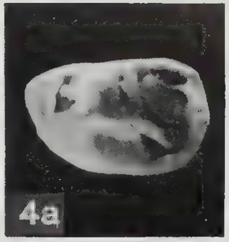
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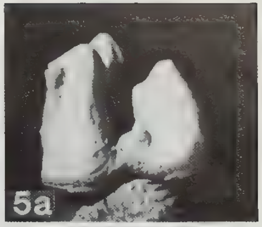
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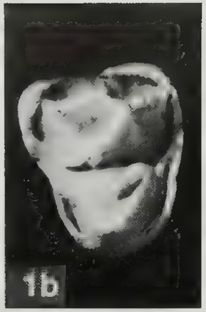
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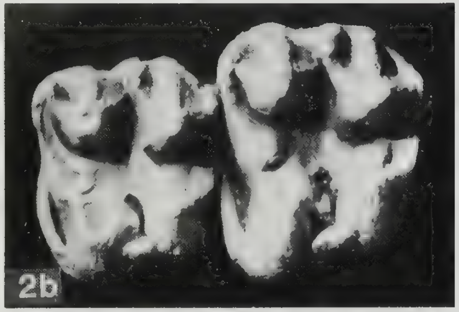
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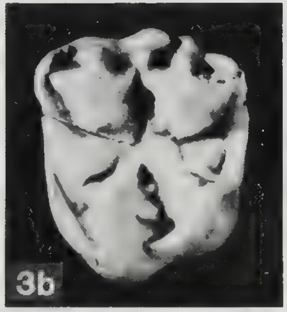
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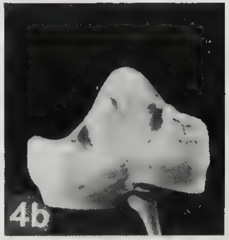
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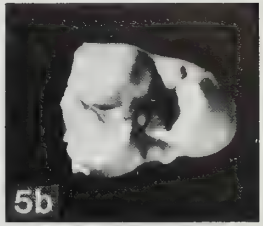
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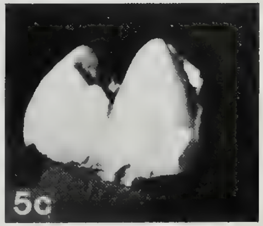
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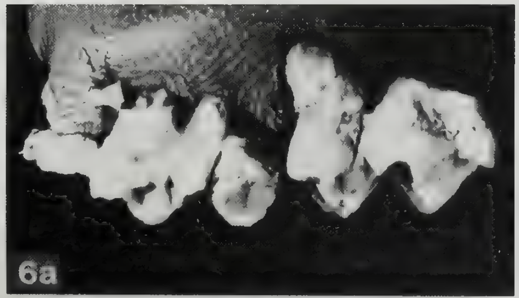
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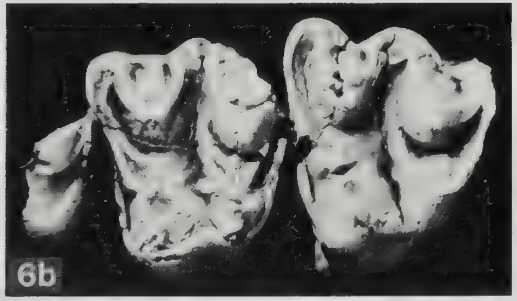
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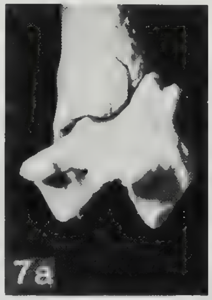
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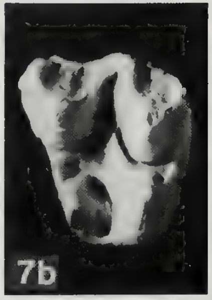
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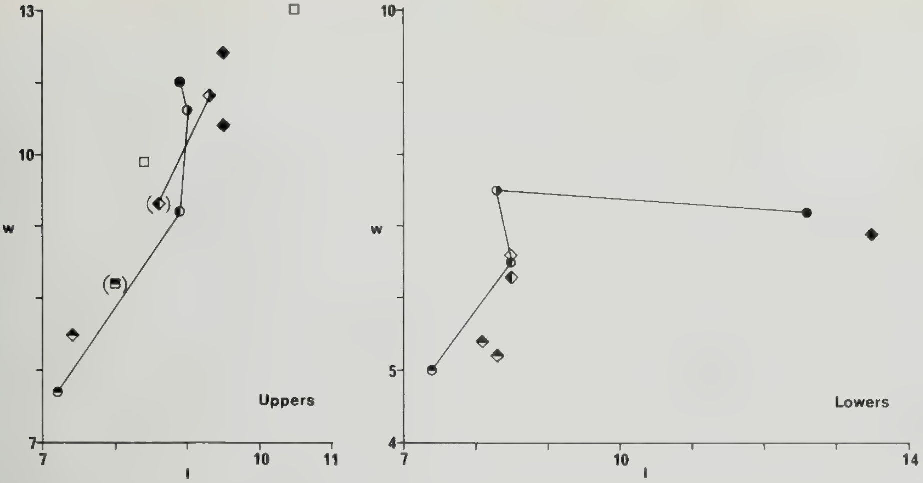

Text-figure 63 Scatter diagrams of length (l) against width (w) in upper and lower cheek teeth of species of *Haplobunodon*. Measurements in millimetres. Width of lower molariform teeth is talonid width. ◇ = *H. venatorum* sp. nov. from Creechbarrow; □ = *H.* aff. *venatorum* from Mormont; ○ = *H. lydekkeri* Stehlin from Hordle Cliff. Symbols solid above = P4; solid on left = M1; solid on right = M2; completely solid = M3; outline = M1/2. Lines join teeth of one individual.

M37528 has all the distal half and the lingual edge broken away. It resembles M37712 in what remains of the cingula, although the parastyle appears more weakly crested and it is less worn. A very worn right P^4 of *Haplobunodon* from Mormont (LGM 9157: LM 797, figured Stehlin, 1908: pl. 13, fig. 36) resembles M37712 except in that it is slightly larger, has more papillate cingula and the ectocingulum is more continuous.

M^{1-2}: Two preultimate molars which were found in the same bag of matrix, and whose interstitial facets match (M37529) are the only ones identified with certainty as being either tooth. M^2 is larger than M^1 and less worn. The ectocingulum is so weak on M^2 that it is nearly missing (M^1 is abraded in this area). The lingual cingulum in both is restricted to a short stretch between the protocone and metaconule. M37713 is broken but almost unworn, has a small ?hypostyle at the distal end of the postmetaconule crista, an almost complete cingulum round the metaconule and a low ridge in the valley, between the protocone and metaconule, which may represent a prehypocrista. Of three $M^{1/2}$s of *Haplobunodon* from Mormont (figured Stehlin, 1908: pl. 13, figs 16, 36 and 41) the last has thin enamel and is low-crowned, and is thus here reidentified as a DP^4. Of the remaining two, LGM 9166: LM 852 is the same length but slightly broader than the M37529 M^1 and has an almost complete ectocingulum; and LGM 9146: LM 854 is larger in both dimensions than the M37529 M^2, has a complete papillate ectocingulum, a faint postcingulum and signs of a prehypocrista.

M^3: This tooth varies in outline shape from being like the M^{1-2}s (M37529) to distally attenuated (M37531). The lightly worn example, M37529, can be distinguished from M^{1-2}s in

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Plate 33 Light macrographs of cheek teeth of *Haplobunodon* and *Dacrytherium* from Creechbarrow, × 3. Figs 1a, 2a, 3a, 5a, 6a, 7a are buccal views. Figs 1b, 2b, 3b, 4a, 5b, 6b, 7b are occlusal views. Figs 4b, 5c are lingual views.

Figs 1–5 *Haplobunodon venatorum* sp. nov. Fig. 1a, b, right P^4 (reversed) (M37712). Fig. 2a, b, right M^{1-2} (reversed) (M37529). Fig. 3a, b, right M^3 (reversed) (M37533). Fig. 4a, b, right P_4 (reversed) (M37541). Fig. 5a–c, left M_3 talonid fragment (M37545). See p. 404.

Figs 6–7 *Dacrytherium elegans* (Filhol). Fig. 6a, b, right M^{1-3}, M^1 fragmentary (reversed) (M37717). Fig. 7a, b, left $M^{1/2}$ (M36814). See p. 410.

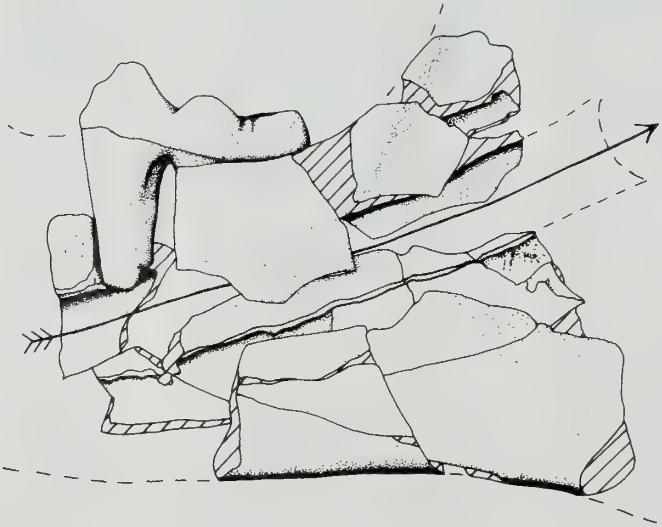
having the metacone lower than the paracone. M37531 also has a buccally salient metastyle. There is also variation in strength of the ectocingulum.

P_3: M37539 preserves only the distal half. Quite a large metaconid appears to have been present. The postprotocristid trifurcates, only the convex buccal limb reaching the distal tooth margin, where there is a small cusp. *H. solodurense* is similar but has no metaconid (Stehlin 1908: pl. 14, fig. 48; 1910*b*: pl. 20, figs 10, 62). *H. lydekkeri* (BM(NH) 29713) has no metaconid and only a single straight postprotocristid. The characters, inasmuch as they are constant for three specimens of *H. solodurense*, are considered to have specific value.

P_4: The two complete specimens both have very small entoconids but vary considerably in size of paraconid and metaconid although retaining the same relative sizes of these cusps. In the holotype (M37540), the paraconid is a large swollen cusp, slightly worn, but which was probably nearly as tall as the protoconid; the metaconid is a much narrower cusp; and the valley between this and the paraconid is very narrow. M37541 is more worn, but the metaconid forms a small distolingual bulge from the protoconid; the paraconid is much less inflated than on M37540; and the valley between the paraconid and metaconid is wide and very shallow. The M37716 P_4 has the paraconid broken away but has a small metaconid like M37541 and a slightly larger entoconid. Three P_4s of *H. solodurense* are constant for the specific differences from *H. venatorum* but vary in the size and position of the paraconid. In NMB Ef245 it is nearly as large as in M37541 but less lingual with respect to the protoconid (see Stehlin 1908: pl. 14, figs 35, 48; 1910*b*: pl. 20, fig. 55).

Lower molars: No tangible morphological differences between this and the other *Haplobunodon* species have been detected. In *H. venatorum* there is slight variation in size of the ectostylid. In M_3 there is also slight variation in the orientation of the mesial hypoconulid crest (longitudinal or oblique) and the position of its attachment mesially: midway between the hypoconid and entoconid in M37544–5 and M37715, or directly to the hypoconid by way of the postcristid in M37714.

Mandible: The M_3, M37544, is one of very few specimens found in the field during excavation work at Creechbarrow. It is associated with a shattered piece of mandibular ramus, which shows the configuration in the region of M_3 to have been like that of *H. lydekkeri* (see Text-fig. 64 and Cooper 1928: pl. 2, fig. 2) and *H. solodurense*.



Text-figure 64 Medial view of right mandibular fragment with M_3 of *Haplobunodon venatorum* sp. nov. (M37544) from Creechbarrow. Arrow indicates course of dental canal. × 2·3.

Discussion. Considering the intraspecific variation in the Creechbarrow assemblage, it is probable that most of the Mormont material is conspecific with it, although exact identity is not demonstrable. It will thus be referred to as *H.* aff. *venatorum.* Its age is considered to be Marinesian, based on one specimen labelled 'Eclépens' and none being labelled 'Entreroches'. The small upper molar from Entreroches (NMB Mt373; see Stehlin 1908: pl. 13, fig. 33; note that this is mislabelled in his plate legend as LM 853) is outside the range of size variation expected for *H. venatorum* and coincides closely with the size of *H. solodurense.*

The species morphologically closest to *H. venatorum* appears to be *H. solodurense* from the late Lutetian–Auversian of Egerkingen. It would be possible to derive the former from the latter by increase in overall size and also in premolar molarization, including the curious enlargement of the paraconid. However, there appear to be no temporal trends within the Egerkingen assemblages towards *H. venatorum.* Ludian *H. lydekkeri* appears more primitive in its paraconid and is unlikely to be the descendant of *H. venatorum. H. muelleri* appears to be more distantly related, as its jaw characters are not shared with the other three species. On this basis and on the presence of P_1 in *H. muelleri,* Stehlin (1910*b*: 1112) considered that it might eventually be placed in a separate genus. Unfortunately, all others except the type species are too incomplete to know whether they had $P\frac{1}{1}$.

Family ?**CHOEROPOTAMIDAE** Owen 1845 (*sensu* Sudre 1978*b*)

Genus ?*CHOEROPOTAMUS* Cuvier 1822

?***Choeropotamus*** sp. indet.

vp. *1980 Choeropotamus* spp.; Hooker & Insole: 44.

Material. Fragment of right P^2? (M37563) and fragment of right P^4? (M37566).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. M37563 is broken mesially and distally, has a narrow wedge-shaped outline, one large cusp bordered by strong cingula and a very rugose surface. M37566 could be a distal fragment of P^4; it is more finely rugose than M37563, has a strong papillate cingulum continuous throughout the preserved edge and a slightly papillate crest which might be a postparacrista. Neither fragment fits any other taxon recorded from Creechbarrow but both resemble *Choeropotamus* in size, apparent bunodonty, enamel rugosity and probable outline. Size would correspond with *C. lautricensis* from the Marinesian of France. The identification is intended to be only very tentative, however. Both teeth are so fragmentary that no definite identification should be made even to ordinal level.

Superfamily **ANOPLOTHERIOIDEA** Bonaparte 1850
(rank emend. Romer 1966) (*sensu* Sudre 1978*b*)

Family **ANOPLOTHERIIDAE** Bonaparte 1850 (*sensu* Viret 1961)

Diagnosis. See Viret (1961: 935).

Subfamily **DACRYTHERIINAE** Depéret 1917
(rank emend. Viret 1961)

Type genus. *Dacrytherium* Filhol 1876*a.*

Included genera. *Catodontherium* Depéret 1908, *Leptotheridium* Stehlin 1910*b* and *Tapirulus* Gervais 1850.

Range. Middle Lutetian–early Stampian, Europe.

Diagnosis. See Viret (1961: 936).

Genus *DACRYTHERIUM* Filhol 1876*a*

[incl. *Plesidacrytherium* Filhol 1884; for more detailed synonymies see Stehlin, 1910*b*: 882–900.]

Type species. *D. cayluxi* Filhol 1876*a*. Early Ludian limestone; Lamandine, Quercy, France. Following Stehlin (1910*b*: 843) this species is almost universally synonymized by authors with *D. ovinum* (Owen 1857*b*), from the Lower Headon Beds of Hordle Cliff, Hampshire (not the Isle of Wight as originally stated by Owen, 1857*b*, and followed by Stehlin, 1910*b*, and Sudre, 1978*b*).

Included species. *D. saturnini* Stehlin 1910*b*; *D. priscum* Stehlin 1910*b*; *D. elegans* (Filhol 1884) Stehlin 1910*b*; and *D.* cf. *elegans*.

Range. Middle Lutetian to Ludian; England, France and Switzerland.

Diagnosis. See Sudre (1978*b*: 110).

Dacrytherium elegans (Filhol 1884) Stehlin 1910*b*

(Pl. 33, figs 6–7; Text-fig. 65)

v. *1977b* *Dacrytherium* sp.; Hooker: 141.
v. *1980* *Dacrytherium* sp.; Hooker & Insole: 44.

Holotype. Cranial fragment with P^3–M^3. Early Ludian limestone; Lamandine-Haute, Quercy, France (Filhol 1884: 191–192; pl. 10, figs 5–6).

Range. Marinesian, England, France and Switzerland; early Ludian, France.

Material. Distal fragment of right P^3 (M37564); right M^1 (fragmentary)–M^3 (M37717); left $M^{1/2}$ (M36814); right lower canine? (M37548); left P_2 (M37718); and fragment of lower deciduous premolar? (M36197).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Emended diagnosis (essentially following Stehlin's 1910*b* description). Small *Dacrytherium* (mean length of M^1 = 8·0 mm). Upper molars strongly dilambdodont, with mesostyles broadly looped. Preorbital fossa shallow and restricted in extent.

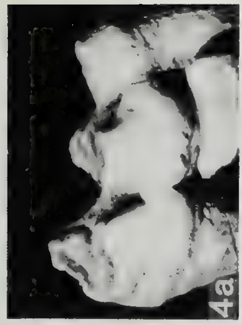
Discussion. The important character of the preorbital fossa obviously cannot be recognized when only teeth or jaws are available. This is the case with the Creechbarrow material. The pre-Marinesian species *D. priscum* and *D.* cf. *elegans* can be excluded from consideration since they are less dilambdodont. The teeth of the remaining species, however, appear to be only separable on size (see Sudre 1978*b*: 110). Text-fig. 65 is a scatter diagram of length against width of various upper molars of strongly dilambdodont species (mainly from published measurements). The Creechbarrow molars fit well with *D. elegans* from both the type locality and Eclépens-Gare. There is overlap, especially of M^1, with the slightly smaller *D. saturnini*, which appears otherwise to differ only in low size increase from M^1 to M^3 and in low length and high width variation of M^1. This species, according to Stehlin (1910*b*: 929), has a deep preorbital fossa like *D. ovinum*, but the material used here for size comparison is from Ste Néboule (Sudre 1978*a*: 278), where no specimen with a preorbital fossa preserved is recorded.

Plate 34 Light macrographs of cheek teeth of *Haplobunodon* and *Dichodon* from Creechbarrow, × 3. Views are buccal (a), occlusal (b or unsuffixed) and lingual (c).

Figs 1–4 *Haplobunodon venatorum* sp. nov. Fig. 1a–c, distal half of right P_3 (reversed) (M37539). Fig. 2a–c, **holotype** right P_4 (reversed) (M37540). Fig. 3a–c, left P_4 (paraconid broken), M_1 and trigonid fragment of M_2 (associated) (M37716). Fig. 4a–c, right M_3 (reversed) (M37544). See p. 404.

Fig. 5a–c *Dichodon* cf. *cervinus* (Owen). Left M_3 (hypoconulid broken) (M37549). See p. 413.

Fig. 6 *Dichodon* sp. indet. Distal fragment of left DP^2 (M37562). See p. 414.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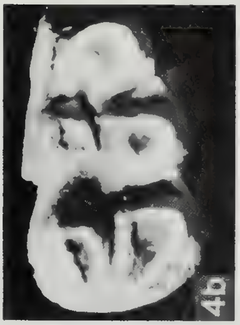
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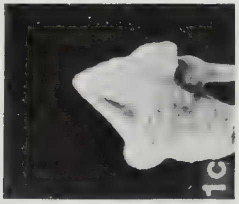
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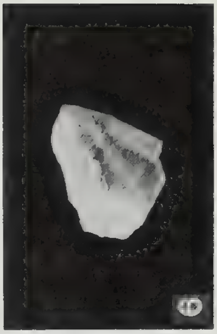
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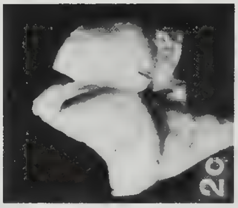
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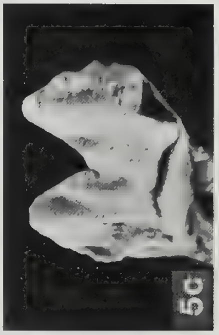
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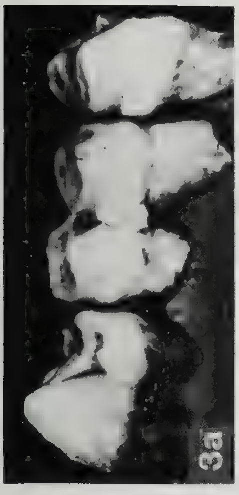
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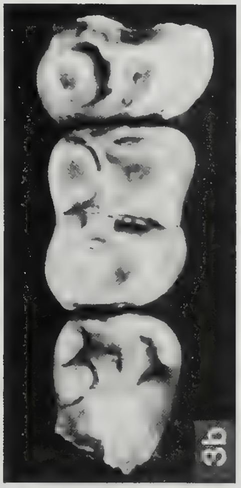
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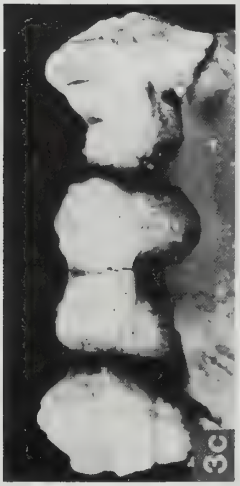
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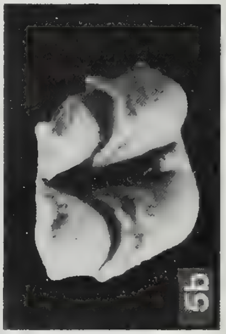
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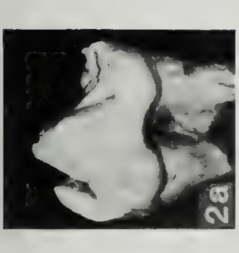
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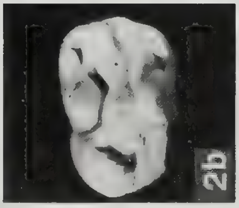
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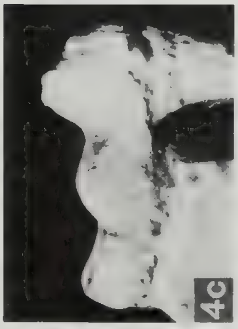
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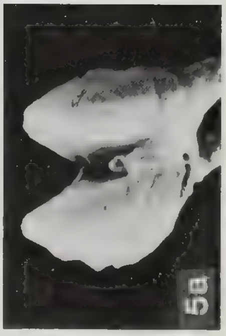
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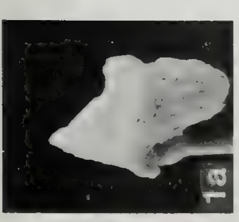
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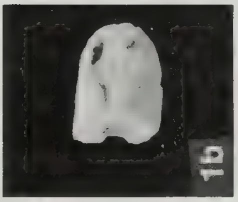
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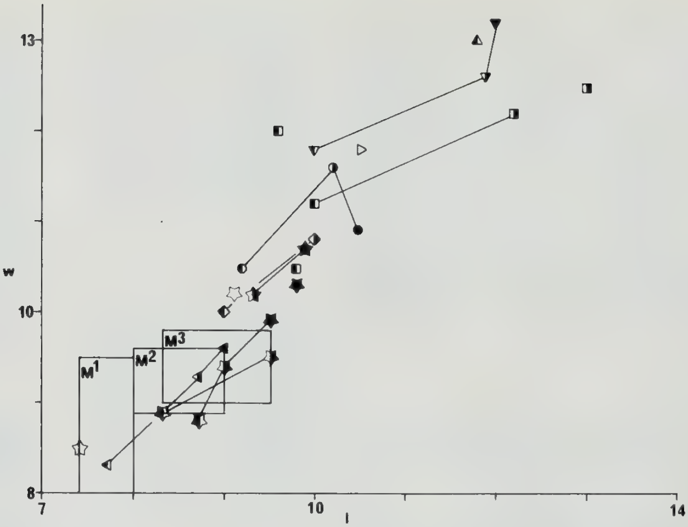


Text-figure 65 Scatter diagram of length (l) against width (w) in upper molars of species of *Dacrytherium*. Measurements in millimetres. Large rectangles delimit *D. saturnini* Stehlin from Ste Néboule (from Sudre 1978*a*: 278). ○ = Lamandine; □ = Fons 4; ◇ = Fons 5; △ = Perrière; ▽ = Euzet (these three localities from Sudre 1978*b*: tab. 11); ▷ = Eclépens B (from cast); (all *D. ovinum* (Owen) and *D.* sp. nov.?). ☆ = Creechbarrow; ☆ = Eclépens-Gare (from cast and Stehlin 1910*b*: pl. 16, fig. 10); ◁ = Lamandine (from Stehlin 1910*b*: text-fig. 158); (all *D. elegans* (Filhol), holotype from Lamandine). Symbols solid on left = M^1; solid on right = M^2; completely solid = M^3; outline = $M^{1/2}$. Lines join teeth of one individual.

The plots, especially of M^1s, in Text-fig. 65 also show a cluster larger than *D. ovinum* and discretely separate from it. Perhaps this represents an undescribed species. On morphological grounds, Stehlin's (1910*b*) '*D.* cf. *elegans*' from Egerkingen definitely requires a new specific name.

Suborder **TYLOPODA** Illiger 1811

Superfamily **XIPHODONTOIDEA** Flower 1884
(rank emend. Viret 1961)

Family **XIPHODONTIDAE** Flower 1884

Type genus. *Xiphodon* Cuvier 1822.

Included genera. *Paraxiphodon* Sudre 1978*b*, *Haplomeryx* Schlosser 1886 and *Dichodon* Owen 1848*a*.

Range. Late Lutetian–late Ludian, Europe.

Diagnosis. See Sudre (1978*b*: 128).

Genus ***DICHODON*** Owen 1848*a*

Type species. *D. cuspidatus* Owen 1848*a*. Lower Headon Beds, Hordle Cliff, Hampshire.

Included species. *D. cervinus* (Owen 1841) Owen 1857*a*, *D. stehlini* Sudre 1973, *D. frohnstettensis* Meyer 1852, *D. simplex* Kowalevsky 1874, *D. subtilis* Stehlin 1910*b*, *D. cartieri* Rütimeyer 1891, *D. lugdunensis* Sudre 1972, *D. ruetimeyeri* Stehlin 1910*b*. See Stehlin (1910*b*), Depéret (1917), Dechaseaux (1965) and Sudre (1972, 1973, 1978*b*) for details of this genus. It is evident from the suffix of the name of the type species that Owen (1848*a*) intended *Dichodon* to be masculine in gender, following that of the Greek original. Contrary to the common practice of authors, the suffixes of the other relevant adjectival species names listed above have been altered to make them agree.

RANGE. Late Lutetian–late Ludian, England, France, Switzerland and Spain.

DIAGNOSIS. See Stehlin (1910*b*: 1011–1017).

Dichodon cf. ***cervinus*** (Owen 1841) Owen 1857*a*

(Pl. 34, fig. 5)

vp. *1977b* *Dichodon* sp.; Hooker: 141.
vp. *1980* *Dichodon* sp.; Hooker & Insole: 45.

HOLOTYPE of *D. cervinus.* Left horizontal ramus containing M_{1-3}, with anterior edge of ascending ramus and detached piece of angular region (IGS GSM916). Shelly sandstone bed in Osborne Beds; Binstead, Isle of Wight. It has been figured by Pratt (1835: figs 1–2) and Owen (1846: 440, fig. 181).

RANGE of *D. cervinus.* Ludian, England, France, Switzerland and Spain; cf. Marinesian, England and Switzerland; aff. Marinesian, France.

DIAGNOSIS of *D. cervinus.* The species appears never to have been formally diagnosed. The best idea of its specific characters can be gained from the detailed descriptions of the type by Owen (1841, 1846) and of referred material by Stehlin (1910*b*: 1019–1021), Depéret (1917: 148–158; pl. 20) and Dechaseaux (1965).

MATERIAL. Left M_3, broken distally (M37549).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. A slight distal bend to the distobuccal wall of the hypoconid immediately preceding the distal truncation of the tooth indicates an M_3 (rather than an M_1 or M_2) from which the hypoconulid lobe and the distal part of the entoconid have been broken away.

Although it is not appropriate herein to rediagnose the two English *Dichodon* species (*D. cuspidatus* and *D. cervinus*), the principal differences between them are important to identification of the Creechbarrow specimen. In the former: 1, size is greater; 2, the upper molar parastyle, double mesostyle and metastyle are larger and more buccally salient; 3, the lower molar parastylid, metastylid, entoconulid and entostylid are larger and more lingually salient; and 4, the upper molar protocone and hypocone are as close together as the paracone and metacone instead of being wider apart (making the outline of the tooth taper lingually rather than be equiangular). Characters 2 and 3 are functionally linked by the occlusal relationships of the upper and lower teeth. Character 4 should result in the lower molar entoconid being smaller in *D. cuspidatus* than in *D. cervinus*, but I have not seen the necessary unworn specimens to verify this. It should be pointed out here that *D. stehlini* from La Débruge, which was thought to be derived from *D.* 'cf. *cervinus*' by Sudre (1973), was differentiated by him from *D. cuspidatus* on morphological features which appear to be variable within the type assemblage of the latter. In fact in character 4 above it is closer to *D. cuspidatus* than to *D. cervinus*. However, the upper molar from Robiac referred to *D.* aff. *cervinum* (Sudre 1969*a*: 135, fig. 18a) resembles *D. cuspidatus* in character 4.

M37549 fits *D. cervinus* in characters 1 and 3. Its talonid is narrower than its trigonid (7·2 mm for the trigonid, 6·7 mm for the talonid) and the length of the tooth minus the hypoconulid lobe is 8·9 mm. The same measurements of M_3 of the holotype of *D. cervinus* are 6·8 mm, 6·4 mm and 9·6 mm respectively. As in this specimen, the lingual stylar cuspids are relatively weak compared with those of *D. cuspidatus* (see Pl. 34, figs 5b–c).

Other details of M37549 are probably of an individual nature. The cristid obliqua extends deep into the valley between the metastylid and entoconulid, whereas the protocristid terminates more buccally. There is a short pillar-like ectostylid just lingual to the buccal tooth edge, with a thin enamel crest extending lingually a short distance from it.

Stehlin (1910*b*) recorded *D.* cf. *cervinus* from Mormont at both 'Station d'Eclépens' and 'Entreroches'. The Creechbarrow specimen tentatively supports a long range for this species from the Marinesian to the late Ludian.

Dichodon sp. indet.

(Pl. 34, fig. 6)

vp. *1977b* *Dichodon* sp.; Hooker: 141.
vp. *1980* *Dichodon* sp.; Hooker & Insole: 45.

MATERIAL. Distal fragment of left DP^2 (M37562); and left hypoconid fragment? (M37719).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. M37562 shows a metacone, swollen metastyle and a distal cingulum. There is no buccal cingulum on the part of the buccal edge preserved. In size it compares closely with that of two DP^2s of *D. cuspidatus* from the Lower Headon Beds of Hordle Cliff (BM(NH) 25248X and M25100). In morphology it is very close to the former (see Owen 1848*a*: pl. 4, figs 2, 3, 5), although it shows slightly more wear. M25100 shows no metastylar swelling and is overall a more strongly crested tooth.

M37719 is identified as an M_3 hypoconid as it appears broken mesially and distally at the junctions of adjacent tooth lobes. It is only slightly worn and gives a good idea of the crown height, which compares fairly well with similarly worn examples of *D. cuspidatus*. It differs, however, from M37549 in being intermediate in size between *D. cuspidatus* and *D. cervinus*.

These two specimens indicate the presence of a species different from *D.* cf. *cervinus*, which may be related to *D. cuspidatus*. However, better material is needed.

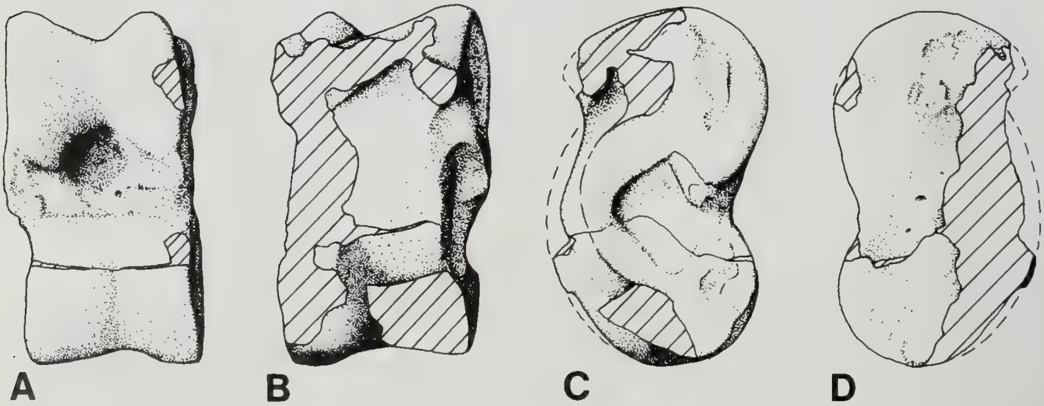
Artiodactyla indet.

(Text-fig. 66)

MATERIAL. Right astragalus (M37567).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. Length is 9·9 mm, width of the tibial trochlea 5·0 mm and width of the trochleated head 4·7 mm. The bone is relatively straight-sided and elongate in dorsal or plantar views and it has deep dorsal and lateral cavities. The apparent shallowness of the tibial trochlea and absence of a ridge separating the cuboid and navicular facets on the trochleated head (the latter typically an advanced ruminant character) are probably the result of post-mortem abrasion.



Text-figure 66 Right astragalus of indeterminate artiodactyl (M37567) from Creechbarrow. Views: A, dorsal; B, plantar; C, lateral; D, medial. × 5.

The elongation and straightness together with the deep lateral cavity are characters found in the Xiphodontidae. The only xiphodont genus small enough is *Haplomeryx*, which is unknown from teeth at Creechbarrow. An astragalus of this genus from Euzet is poorly figured by Depéret (1917: pl. 19, figs 32–33). Creechbarrow artiodactyl taxa represented by teeth, of appropriate size for this astragalus, are *Hyperdichobune* sp. 1 (p. 376), *Cebochoerus robiacensis* (p. 398) and *Acotherulum campichii* (p. 400). Astragali are unknown for these genera. The only dichobunid astragali appear to be those attributed to *Protodichobune* by Teilhard (1922: pl. 3, figs 24–25) and *Messelobunodon* (Franzen 1981: 313). The former has a narrow neck and trochleated head only slightly more advanced than the primitive earliest Eocene diacodexids. The latter also has the trochleated head narrower than the tibial trochlea.

The specimen must remain indeterminate below ordinal level but there is a possibility that it may eventually prove to belong to one of the small cebochoerids in the fauna.

Correlation

Range of the Bartonian in England

Concepts of the stage. Mayer-Eymar (1857) originally based his Bartonian Stage on successions in the Hampshire, Paris and Belgian basins. He later (1869) removed the Marnes à *Pholadomya ludensis* from the top of his Bartonian and Munier-Chalmas & Lapparent (1893) erected the Ludian Stage to include these plus the higher Gypse beds. Lapparent later (1906) retracted the Ludian. The legacy of this indecision and of the problems of correlation between the three basins of the type area has been fifteen different concepts of the Bartonian (Feuillée 1964). The large number of substages erected by authors (see Feuillée 1964: 40) in the Paris Basin have become restricted by general usage to two; the Auversian and Marinesian (see Pomerol 1980), the Ludian often being treated as an independent stage (especially by palaeomammalogists; see Cavelier 1980). All three have been widely used in correlating outside the Paris Basin despite the restricted nature of much of their aquatic invertebrate faunas.

The late Eocene Priabonian Stage (Munier-Chalmas & Lapparent 1893) was erected in Italy and has often been used since as a synonym of the Bartonian. Cavelier & Pomerol (1976) showed instead that the Priabonian was essentially equivalent to the Ludian and therefore succeeded the Bartonian, and was the terminal stage of the Eocene. The Eocene being now divisible into four main stages (Ypresian, Lutetian, Bartonian and Priabonian), problems arose as to where the Middle–Upper Eocene boundary should be drawn. The Bartonian was usually placed in the Upper Eocene when there were considered to be only three main stages, but Hardenbol & Berggren (1978) relegated it to the Middle as it was contemporaneous with planktonic foraminiferal zones normally placed in the Middle Eocene. These authors also preferred to define Palaeogene stages on planktonic foraminiferal zones because these were best for long range correlation. They equated the Bartonian with P13–14 (≡ NP16 upper–17).

Curry (1981) has argued that historically the cliffs near Barton, rather than localities in the Paris Basin as advocated by Morellet & Morellet (1934), should more correctly be considered stratotype of the Bartonian Stage. He proposed that the stratigraphical extent of the stage at the stratotype should correspond to the 'Barton Beds' as emended by Keeping (1887). The base could thus be defined biostratigraphically by the incoming of *Rhombodinium draco*, but the top only by the relatively local and uncorrelatable environmental change of marine to non-marine conditions.

The strata in England that Mayer-Eymar (1857) placed in his Bartonische Stufe were: 'white sands of Headon Hill, series of clayey and sandy beds of Alum Bay and clays of Barton' (translation). It is evident that his upper boundary was not in doubt here as he listed 'freshwater formation of Hordwell and of Headon Hill, Alum Bay and Totland Bay' in the Ligurian Stage, beds which conformably overlie the Headon Hill Sands (herein Becton Sand Formation). His lower boundary, however, is in doubt in England for two reasons. Firstly, he indicated a gap with a '?' in the upper part of the underlying Parisian Stage (s.s. = Lutetian), above 'sands and marls of Bagshot … and of Bracklesham'. Secondly, his 'clayey and sandy beds of Alum

Bay' are unidentifiable in detail but must include strata lower than just the Barton Clay at Alum Bay, since the Headon Hill Sands are already accounted for. His lower boundary in the Paris Basin was, however, not in doubt: it was between the 'marls and caillasses' (Upper Calcaire Grossier; Lutetian) and the 'sands of Beauchamp and Auvers' (Bartonian).

In erecting stages, Mayer-Eymar, like many other 19th Century workers, was essentially using fossils as worldwide time markers, but biostratigraphic successions were then too incomplete to give clear boundaries. Lithostratigraphic boundaries were thus relied upon for the stage (time) boundaries. Current French usage of the Bartonian substages Auversian and Marinesian (which together constitute Mayer-Eymar's concept of the English and northern French Bartonian after he had removed the Marls with *Pholadomya ludensis* in 1869) comprise sedimentary cycles which are not easy to correlate *per se* outside the local area. Hardenbol & Berggren's (1978) solution of using planktonic foraminiferal zones for defining the Bartonian allows ready use of a chronostratigraphic term over a wide area of the globe. However, this cannot be extended to the type area where the P zones are unknown, and their extrapolated positions using the intermediaries of dinocysts and sparse calcareous nannoplankton occurrences are likely to be inaccurate, although the NP16/17 boundary has recently been shown to occur between Barton beds B and E (Aubry 1983). On the basis of the name, it is accepted that the type locality of the Bartonian Stage should be the area of Barton. However, to follow Mayer-Eymar's type boundaries, it is necessary to consider the Paris Basin succession. If one accepts the Calcaire Grossier/Sables Moyens junction as the lower boundary and the removal of the Marls with *Pholadomya ludensis* from the top by Mayer-Eymar (1869), their correlatives in the Hampshire Basin would be the base of the oldest Barton Clay (as emended herein) for the lower boundary and the top of Barton bed I of the Becton Sand Formation for the upper boundary (see pp. 204–205).

These are the limits of the Bartonian followed herein (Auversian–Marinesian). With these boundaries, biostratigraphic correlation outside the north-west European basins would still be a problem, but which magnetostratigraphy (see Aubry 1983: fig. 35) and possibly the recognition of worldwide discontinuities reflecting sea level changes (see Vail & Hardenbol 1979) may eventually resolve.

Curry's (1981) recent restriction of Bartonian at the stratotype may turn out to be more useful biostratigraphically, since the incoming of *Rhombodinium draco* in the Anglo-Paris Basin area may approximate the base of P13. The evidence for this is the recognition in the Kallo borehole (Belgium) of basal NP16 near the base of the Argile d'Asse (Martini 1971) and a dinocyst assemblage *c.* 20 m higher in the same formation, suggesting to Châteauneuf (1980: 292) correlation with the upper Auversian of the Paris Basin and 'Lower Barton Beds' of Hampshire. This is further supported by Aubry's (1983) study of calcareous nannoplankton in the Hampshire and Paris Basins. In such a case much of the Auversian would have to be relegated to the Lutetian.

The lower limit of the Auversian in England. The lower limit of the Auversian in the Paris Basin corresponds with the base of the Formation de Mont St Martin. The strata in England which were long correlated with the whole of the Sables Moyens (Auversian) are the *Nummulites variolarius*-bearing 'Upper Bracklesham Beds' (= Selsey division of Curry *et al.*, 1977), e.g. by Wrigley on molluscs and Chandler on plants. The correlation was based on common occurrence in both strata of the foraminiferid *Nummulites variolarius*. It was not until Curry (1962) discovered *N. variolarius* in the Paris Basin Lutetian that this correlation was seriously questioned. Curry later (1967) equated only the upper part of the *N. variolarius*-bearing 'Upper Bracklesham Beds' (= upper Selsey division of Curry *et al.* 1977) with the Auversian, on the basis of the best statistical comparison of the mollusc faunas. Curry *et al.* (1978: 43) took a compromise position between the more extreme views of Pomerol (1961, 1964) on the one hand and of Morellet & Morellet (1948) and Curry (1967) on the other, and equated the Huntingbridge division (the topmost) of the Bracklesham Beds (= Elmore Member of the Barton Clay Formation herein), with the Auversian. *N. variolarius* does not occur in England above the Selsey division but this nummulite has now generally been abandoned as a means of correlating the Auversian, because of its extended range outside this substage and its geographically restricted Bartonian occurrence.

The solution of Curry *et al.* (1978) is supported by ostracod faunas (see Keen 1978: 438–439) and is followed here. Thus base Elmore Member of the Barton Clay Formation ≡ base Auversian.

The upper limit of the Marinesian in England. The Barton Clay with its rich molluscan fauna has usually been correlated with the Sables de Cresnes and adjacent beds in the Paris Basin and therefore considered Marinesian (e.g. Morellet & Morellet 1948). Curry (1967), on the basis of the molluscs, placed only the 'lower Barton Beds' in the Marinesian. Other views have placed the 'Barton Beds' as low as the Auversian (Pomerol 1973) or as high as the Ludian (Pomerol 1964). The occurrence of species typical of the standard Calcareous Nannoplankton Zone NP17 in bed H (the upper part of which is defined here as the base of the Becton Sand Formation) aids correlation with more distant parts of the world but not with the Paris Basin (Martini 1971).

The Marnes à *Pholadomya ludensis* (type basal Ludian) represent a widespread but short-lived marine transgression in the Paris Basin and have a restricted fauna consisting largely of either long-ranged or endemic forms. Strata in England correlated with them have ranged from Barton Clay (Wrigley & Davis 1937) to Brockenhurst Bed (basal Middle Headon Beds) (Krutsch & Lotsch 1964). Curry (1967: 457) noted the occurrence of the gastropod *Turritella elongata* in both the Marnes à *Pholadomya ludensis* and 'near the boundary of the Middle and Upper Barton Beds' [Bed G?], although his chart (fig. 5) indicates correlation with lower parts of the 'Barton Beds'. Keen (1978: 439) suggested general correlation of the 'Barton Beds' with the Marnes à *Pholadomya ludensis* on the basis of ostracods, but he was not able to use this group to subdivide the former strata.

Châteauneuf (1980: 290) correlated the Middle Headon Beds with the Marnes à Lucines (overlying the Marnes à *Pholadomya ludensis*) and beds C–F of the Barton Clay with the Sables de Cresnes, using dinocyst evidence combined from his own work in the Paris Basin with that of Bujak *et al.* (1980) in the Hampshire Basin. This M. Headon Beds ≡ Marnes à Lucines correlation is also supported by ostracods (Keen 1978: figs 2–3). Grambast (1964) correlated the Lower Headon Beds with higher parts of the Marnes à *Pholadomya ludensis* on the basis of charophytes.

As the transgression of the basal Marnes à *Pholadomya ludensis* is very widespread in the Paris Basin and yet also very short-lived, it was probably allocyclically generated. An equally short-lived transgression within the Barton Clay and Becton Sand Formations and occurring between Barton Clay bed F and the base of the Middle Headon Beds is that of bed J, which forms the lower part of the fifth sedimentary cycle described below. The top of the fourth cycle (top of bed I in Christchurch Bay) is therefore here somewhat tentatively taken as the top of the Marinesian in the central Hampshire Basin succession.

The Auversian–Marinesian Boundary in England. As mentioned above, Curry *et al.* (1978) correlated the lowest parts (cycles 1 and 2) of the Barton Clay Formation (as 'Huntingbridge Formation') with the Auversian and much of the rest of the Barton Clay Formation (as 'Barton Beds') with the Marinesian, thus indirectly indicating a boundary correlation although the details of this were probably not intended. Châteauneuf (1980: 289–290, 302; text-fig. 50) correlated the *Nummulites prestwichianus* bed of the Barton Clay with an horizon high in the Sables de Beauchamp (Auversian) on the basis of the first occurrence of the dinocyst *Rhombodinium draco* in both (base of *Heteraulacacysta porosa* Assemblage Zone of Bujak *et al.*, 1980; and of the *Rhombodinium intermedium* and *Areosphaeridium dictyoplokos* Zone of Châteauneuf, 1980). He also correlated Barton Clay beds C–F with the Sables de Cresnes on the basis of the *Rhombodinium porosum* assemblage. This means that in the Hampshire Basin the Auversian–Marinesian boundary should lie somewhere between beds A1 and C at Barton Cliff. The complex of Marinesian strata below the Sables de Cresnes in the Paris Basin (Sables d'Ezanville, Calcaire de Ducy, Sables de Mortefontaine, Calcaire de St Ouen) are almost devoid of dinocysts, their nannoflora is species poor and their mollusc faunas are essentially non-marine and long-ranging. Thus correlation in this part of the sequence is very difficult.

Radiometric Dates. Two studies (Odin *et al.* 1978; Hardenbol & Berggren 1978) have provided significantly different time scales. The latter is based on igneous rocks worldwide, the former on sedimentary glauconites in the basins discussed herein. Many of the earlier problems of glauconite dating have been overcome by Odin *et al.* but some still remain (see Fitch *et al.* 1978). The top and bottom of the Bartonian are dated by Hardenbol & Berggren (1978) as 40 and 44 million years BP (Ma) and by Odin *et al.* (1978) as 37 and 40 Ma respectively. Odin *et al.* (1978) dated the *N. prestwichianus* bed of the Barton Clay as 39 Ma. Cavelier (1980) gave a date of 41 ± 2 Ma (K/Ar) on upper Marinesian illites of the Paris Basin. Odin & Curry (1981) repeated the date by Odin *et al.* (1978) for the *N. prestwichianus* bed and gave the base of the Sables d'Auvers and equivalents as between 40·5 and 42 Ma.

Mammal correlation in the Bartonian (*sensu* Mayer-Eymar and Pomerol)

Introduction. The three sites, Elmore, Hengistbury and Barton Cliff, are the only ones in the marine Hampshire Basin sequence of the Bartonian which have yielded mammals. The fourth site, Creechbarrow, which contains the bulk of the species described here, is isolated in the far west of the basin and is dated as Marinesian according to its mammal fauna. Mammaliferous localities frequently occur in marginal areas or in fissure fillings whose direct stratigraphical relationships with standard marine successions are obscure. Mammals tend to be rapidly evolving and consequently their stratigraphical ranges are short. They are thus potentially very useful for correlation, but their rarity, especially in marine sequences, and their tendency towards endemism naturally reduce this utility.

Mammals are often sufficiently abundant in non-marine sequences to allow correlation over large areas, even though the relationships with the nearest marine sequence may not be known in detail. In continental Europe, a particular type of biostratigraphy has developed for the purpose of mammal correlation. This consists of a sequence of faunas, each taking its name from an important locality (e.g. Montmartre or Robiac), which have more recently been referred to as 'niveaux repères' (reference horizons; see Franzen 1968: 160; Hartenberger 1969). Subsequently discovered mammal faunas can either be identified with an existing fauna or given a name of their own and slotted into the sequence. The system was pioneered by Thaler (1965, 1966, 1972) and is also discussed by Savage & Russell (1977). One drawback to the system is the frequent reliance on evolutionary grade to determine position in the sequence. This can lead to circularity. In some cases, however, it is virtually unavoidable; e.g. the rich faunas of the Egerkingen fissures in Switzerland are largely unknown in any stratified sequence, marine or non-marine, although there is widespread agreement on their approximate sequential position. Their exact positions, however, do pose problems as they may straddle the Lutetian–Bartonian boundary (see p. 425).

Thaler introduced this system of zonation in an attempt to counter the frequent arbitrary and poorly founded attributions of various mammal faunas to certain marine stages. The latter had previously received a modified usage corresponding in the non-marine provinces to major mammal changes not correlatable with the real marine stage boundaries.

Many localities, which authors often confidently place in sequence with respect to each other, contain only a few species or varieties with known evolutionary polarities (e.g. Lissieu and Le Guépelle; see Ginsburg *et al.* 1965, Sudre 1972, Hartenberger 1972). Moreover, there is little chance of any two mammal localities being exactly the same age, so to refer one to a zone named from another locality gives a false impression of precision in age relationships. The basis for age relationship in biostratigraphy is always identity of named taxa and it seems appropriate to use these for names of zones in the conventional way as used for other groups. Suggestions for the exact order of localities within this framework can be made if no further useful breakdown into subzones can be made.

Niveaux repéres are usually defined either by one or a few index fossils, or by their total faunal list which includes long- as well as short-ranged taxa. Correlation is often made despite absence of the index fossil. The reference of a given locality to a particular concurrent range zone (see Hedberg 1976: 55–57) with a list of the index species on which reference is based would be a more precise method and is advocated here.

Bosma (1974: 99–104) adopted a conventional method of mammalian biostratigraphy by erecting named biozones based on ranges of mammalian taxa rather than on vague faunal assemblages. She also erected the stage name Headonian to incorporate a cogent assemblage of these zones as part of a system of land mammal ages which was extended later to cover the whole of the Tertiary (Fahlbusch 1976). The Headonian corresponds approximately to the Ludian, whilst the next stage below (the Rhenanian) includes not only most of the Bartonian but also the Lutetian and late Ypresian (see also comments by Savage & Russell, 1977).

In the course of this study, the fitting of the relevant mammal faunas directly into the standard Bartonian sequence, without the need for a separate continental chronostratigraphic sequence, seemed possible, although requiring a considerable amount of extrapolation using partial sequences often with little overlap of either lithology or biota. European mammal faunas referable to the Bartonian are few and scattered but several are now known in the Hampshire and Paris basins (Ginsburg *et al.* 1965, Hooker 1972, 1977*b*, Louis 1976). Important fissure fillings occur in southern Germany, Switzerland and France (Dehm 1970, Stehlin 1903, Depéret 1894, Hartenberger *et al.* 1974); and important stratified non-marine sequences in southern France (Garimond *et al.* 1975).

Creechbarrow. The Creechbarrow Limestone Formation (restricted to Creechbarrow) was originally dated as early/middle Eocene because it was thought to be stratified within the pipe-clay series of Dorset which was correlated with the 'Lower Bagshot Beds' (Hudleston 1902*a*, *b*, 1903). The known fossils were algal-coated non-marine gastropods which gave little guide to correlation. Keeping's (1910) discovery of land snails and a '*Palaeotherium*' tooth fragment led him to consider the Creechbarrow Limestone as a mainland outlier of the Bembridge Limestone, which is otherwise restricted to the Isle of Wight. Keeping invented a sequence of beds at Creechbarrow which resembled the same sequence below the Bembridge Limestone on the Isle of Wight (see Arkell 1947). Bloomfield (1911), who had excavated with Hudleston, pointed out that Keeping's section appeared to have been taken from Alum Bay and that there was not enough room for all the strata at Creechbarrow. He ended his letter relevantly: 'Even if the Creechbarrow Limestone fauna and the Bembridge may be identical, they are not necessarily upon the same horizon, and may have existed in Lower Bagshot times. Why not?'

In fact, Keeping's supposed *Palaeotherium* tooth is an indeterminate root? fragment (see Hooker 1977*b*) and in any case the genus *Palaeotherium* ranges from late Lutetian to late Ludian. It is not restricted to beds of Bembridge Limestone age. His '*Dictulumus*' (misprint for *Dichobunus*) tooth (Keeping 1912) is in fact *Lophiotherium*, a genus absent from the late Ludian. Hooker (1977*b*) recorded an extensive mammal fauna from Creechbarrow which was unlike that of the Bembridge Limestone. Preece (1980*a*) revised the molluscs and showed that some of the land snails (e.g. '*Filholia*' *elliptica*) had been misidentified and that only three Creechbarrow species were otherwise known in England only from the Bembridge Limestone. The non-mammal biota of the Creechbarrow Limestone is given below; the mammal list is at the beginning of the systematics section (Table 1, p. 212). Comparable biotic lists for the Bembridge Limestone can be found in Preece (1976, 1981) (terrestrial gastropods); Edwards (1852) (other molluscs, unrevised); Hooker & Insole (1980) (mammals).

This list is based on Hooker (1977*b*) and Preece (1980*a*, 1981). Dr R. Estes identified the Ophidia, Dr A. C. Milner identified the ?lacertilian and Dr P. D. Taylor revised the bryozoan names.

Whereas the typically longer-ranging gastropods have much in common between the Creechbarrow and Bembridge Limestone, the mammals are totally different at species level and moderately different at generic level.

Monera: Cyanophyta indet. (Pl. 35, figs 1–2)

Animalia: Bryozoa (derived from the Chalk)
  Meliceritites sp.
  '*Vincularia*' sp.
  Woodipora sp.
  vinculariiform ascophorans indet.

 Mollusca*–Gastropoda
  Proserpina cf. *woodwardi* Preece 1981
  Cochlostoma heterostoma (Edwards 1852)
  Viviparus angulosus (J. Sowerby 1817)
  V. cf. *lentus* (Solander 1766)
  Bembridgia cincta (Edwards 1852)
  cf. *Coptostylus brevis* (J. de C. Sowerby 1826)
  Lymnaea cf. *longiscata* (Brongniart 1810)
  Palaeoxestina occlusa (Edwards 1852)
  Milax cf. *latus* (Edwards 1852)
  '*Clausilia*' sp.
  Filholia laevolonga (Boubée 1831)
  Palaeoglandina costellata (J. Sowerby 1822)
  cf. *Archygromia durbani* (Edwards 1852)
  Megalocochlea pseudoglobosa (d'Orbigny 1850)
  cf. *Klikia vectiensis* (Edwards 1852)

 Mollusca–Bivalvia
  Unio brightoni Woodward 1965

 ?Arthropoda–?Insecta
  ?Trichoptera larval cases (Pl. 35, fig. 3)
  ?Chironomidae larval tubes (Pl. 35, fig. 1b)
  indet. burrows (Pl. 35, fig. 4)

 Pisces–Teleostei
  Characoidei indet. (teeth) (Pl. 35, fig. 5)
  ?Siluriformes indet. (dermal bones)
  indet. (palatal bones)

 Reptilia–Crocodilia indet. (Pl. 35, fig. 6)

 Reptilia–Chelonia indet.

 Reptilia–Ophidia
  cf. *Cadurceryx* sp.
  indet.

 Reptilia–?Lacertilia indet.

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* References to authors of the molluscan species are to be found in Preece (1980*a*), Hooker (1977*b*) or herein.

Range of Bartonian mammalian taxa and definition of zones. A large number of the Bartonian mammal species have restricted ranges. This is partly geographical but also, more importantly for correlation, stratigraphical. Although many of the localities are not in sequences, the few that are, especially those in marine sequences, show that these ranges are often chronologically short. As an alternative to the 'niveaux-repères' system (p. 418), two mammalian concurrent range zones are erected here to span the late Lutetian and Bartonian. The mammalian zones which Bosma (1974) erected for the Headonian are taxon range zones and concurrent range zones. The concurrent range zones defined here are intended to cover the whole of the west European terrestrial area (with adjacent marine basins included) as it was in Eocene times (see below, p. 449). To achieve this they include a number of taxa, all of which occur together at at least one locality. Because of the general rarity of stratified mammal localities and the isolation of non-stratified ones, neither total ranges nor (in most cases) precise limits of the zones are known. Nevertheless, the taxa defining successive zones do not overlap even in the richest known faunas and their limits may eventually be found to approximate to time horizons.

i. The *Palaeotherium eocaenum–Lophiodon rhinocerodes* Concurrent Range Zone.

This is defined by the total known ranges of *Palaeotherium eocaenum*, *Lophiodon rhinocerodes*, *Lophiotherium pygmaeum*, *Dichobune robertiana*, *Cebochoerus ruetimeyeri*, *Haplobunodon solodurense* and *Pseudamphimeryx schlosseri.*

Various other species whose ranges begin earlier also end at the top of the zone; e.g. *Lophiodon cuvieri*, *L. parisiense*, *Plesiarctomys spectabilis* and *Ailuravus picteti.* See Table 36 for the distribution of the taxa defining the zone. Egerkingen γ and α are the only localities where all the taxa defining the zone occur. The zone ranges from the Upper Calcaire Grossier to the Sables Moyens in the stratified sequence of the Paris Basin.

ii. The *Lophiodon lautricense–Lophiotherium siderolithicum* Concurrent Range Zone.

This is defined by the total known ranges of *Lophiodon lautricense*, *Lophiotherium siderolithicum*, *Palaeotherium lautricense*, *Leptolophus stehlini*, *Acotherulum campichii*, *Haplobunodon venatorum*, *Plesiarctomys hurzeleri*, *Ailuravus stehlinschaubi*, *Xiphodon castrense* and *Simamphicyon helveticus.*

Cebochoerus robiacensis and *Pseudoloris crusafonti* are also restricted to the zone but are not sufficiently widespread to be included. *Lophiodon thomasi* may also be restricted to the zone but

Table 36 Distribution of the taxa defining the Zone of *Palaeotherium eocaenum–Lophiodon rhinocerodes.* Sources: Brunet & Gabilly (1981); Depéret (1906); Franzen (1968); Ginsburg *et al.* (1965, 1977); Louis (1976); Stehlin (1903, 1904*b*, 1905*a*, *b*, 1906, 1908, 1910*a*, 1910*b*); Sudre (1972, 1978*b*); and Wood (1976*a*).

	Pseudamphimeryx schlosseri	*Haplobunodon solodurense*	*Cebochoerus ruetimeyeri*	*Dichobune robertiana*	*Lophiotherium pygmaeum*	*Lophiodon rhinocerodes*	*Palaeotherium eocaenum*
Grès de Brenne, Fonliasmes						×	
Upper Calcaire Grossier, Paris Basin			×	×		×	×
Sables d'Auvers, Le Guépelle							×
'Sidérolithique', Egerkingen γ and Huppersand	×	×	×	×	×	×	×
'Sidérolithique', Egerkingen α	×	×	×	×	×	×	×
'Sidérolithique', Egerkingen β	×	×	×	×	×		×
'Sidérolithique', Lissieu	×			×	×	×	
Calcaire de Castres, Roc de Lunel						×	

Table 37 Distribution of the taxa defining the Zone of *Lophiodon lautricense–Lophiotherium siderolithicum.* Sources additional to those of Table 36: Depéret (1910); Hooker (1977*a*, *b*); Hooker & Insole (1980); Maack (1865); Remy (1965); Stehlin (1918); Sudre (1971); and Wood (1970). Other records are based on information herein and the author's personal observations in museum collections.

	Xiphodon castrense	*Haplobunodon venatorum*	*Acotherulum campichii*	*Palaeotherium lautricense*	*Leptolophus stehlini*	*Simamphicyon helveticus*	*Ailuravus stehlinschaubi*	*Plesiarctomys hurzeleri*	*Lophiotherium siderolithicum*	*Lophiodon lautricense*
Creechbarrow Limestone, Creechbarrow		×	×				×	×	×	
Barton Clay, Hengistbury										cf.
Calcaire de St Ouen, Paris and Grisolles			×							cf.
Sables de Cresnes, Berville										×
'Sidérolithique', Eclépens-Gare	×	aff.	×	×	(×)	×	×	(×)	×	×
Lower Calcaire de Fons, Robiac	×		×		×	×		×	×	×
Sables du Castrais, Le Castrais	×			×	×			×		×
'Sidérolithique', Le Bretou	×					×				
'Sidérolithique', Heidenheim										×

the uniqueness of its occurrence and problems over its exact stratigraphical position require its exclusion. *Anchilophus desmarestii* was considered by Sudre (1969*a*) to be a characteristic Marinesian species, but it also occurs, admittedly with a cf. determination, at Egerkingen where it overlaps with the *eocaenum–rhinocerodes* Zone taxa. A number of fragmentary specimens of a large *Lophiodon* species, usually referred to *L.* cf. *lautricense*, occur at more than one level in marginal calcareous facies cited as being lateral equivalents of the Sables Moyens. They are from Arcis-le-Ponsart (Louis 1976) and Nogent-l'Artaud (Morellet & Morellet 1948), and their horizons have been correlated with the Facies ('Horizon') du Guépelle (Morellet & Morellet 1948) which contains an *eocaenum–rhinocerodes* Zone fauna. The specimens have never been figured or described in detail. Some overlap of the zones may occur, or the records may not represent *L. lautricense* but a different species, or the lithostratigraphic correlation of these marginal facies may not be accurate. A potential immediate ancestor for *L. lautricense* is not known. *L. rhinocerodes* has been discarded from this role by Sudre (1971) and his alternative (*L. cuvieri*) is considered herein (p. 375) to be more closely related and probably ancestral to *L. thomasi*. See Table 37 for distribution of taxa defining the zone.

Eclépens-Gare is the only locality where all the taxa defining the zone occur together. The zone ranges from the Calcaire de St Ouen to the Sables de Cresnes in the stratified sequence of the Paris Basin. The faunal change immediately above this zone is well documented in a stratified non-marine sequence in the Alès Basin, southern France (Garimond *et al.* 1975). There may be a gap between the *lautricense–siderolithicum* Zone and that of *Thalerimys* [*Isoptychus*] *headonensis* (Bosma 1974) Vianey-Liaud 1979, defining the base of the Headonian in southern England. There is room in the earlier Ludian for the faunas of Fons (U. Calcaire de Fons) (Garimond *et al.* 1975).

The *lautricense–siderolithicum* Zone seems to mark a particularly distinctive phase in European Eocene mammal faunas. Of the total of over 100 named and unnamed species-group mammal taxa occurring in this Zone, only 3 range above and below; 14 range only below; 33 range only above; whilst 53 are unknown outside the zone. Of the 53 restricted forms, 8 have likely ancestors in the zone below; 13 have likely descendants in strata immediately above; whilst 2 are sandwiched between respective ancestors and descendants (see Table 38).

Table 38 *L. lautricense–L. siderolithicum* Zone species-group taxa and main localities. The range column indicates occurrence extending below ◐, above ◑, above and below ●, or restricted to the zone ○. ?, aff., or cf. applied to one side or other of the symbol refers to qualification of the earlier or later record(s). Note that *Amphiperatherium ?lamandini* may be the same as *A.* aff. *goethei*, and that Berville, Heidenheim and Hengistbury (not listed) only contain *Lophiodon lautricense* (or cf.). Brackets indicate doubtful provenance. Sources as for Tables 36–37 with addition of Crochet *et al.* (1981).

	Range	Creechbarrow	Barton C–F	Grisolles	Paris	Sergy	Eclépens-Gare	Le Castrais	La Guittardie	Robiac	Le Bretou
Amphiperatherium giselense	●	—	—	×	—	—	—	—	—	—	—
A. minutum	◑	—	—	×	—	—	—	—	—	—	×
A. bourdellense	●	—	—	×	—	—	—	—	—	—	×
A. goethei	◐	aff.	—	—	—	—	—	—	—	—	—
A. lamandini	◑	—	—	×	—	—	—	—	—	—	—
A. fontense	◑	×	—	—	—	—	—	—	—	×	×
Peratherium sudrei	◐	—	—	×	—	—	—	—	—	×	—
P. bretouense	○	—	—	—	—	—	—	—	—	—	×
P. lavergnense	◑	—	—	—	—	—	—	—	—	—	×
Saturninia mamertensis	?◐	—	—	—	—	—	—	—	—	×	×

Table 38 *(continued)*

	Range	Creechbarrow	Barton C–F	Grisolles	Paris	Sergy	Eclépens-Gare	Le Castrais	La Guittardie	Robiac	Le Bretou
S. grisollensis	○	—	—	×	—	—	—	—	—	?	—
S. hartenbergeri	◐	—	—	—	—	—	—	—	—	×	—
S. beata	◑	—	—	—	—	—	—	—	—	—	×
S. grandis	○	—	—	×	—	—	—	—	—	?	—
S. intermedia	?◐	—	—	×	—	—	—	—	—	—	—
Gesneropithex grisollensis	◑ aff.	—	—	×	—	—	—	—	—	—	—
G. figularis	○	×	—	—	—	—	—	—	—	—	—
G. sp. (Robiac)	○	—	—	—	—	—	—	—	—	×	—
Rhinolophus sp. 1	○	—	—	—	—	—	—	—	—	—	×
Vespertiliavus gracilis	◑	—	—	—	—	—	—	—	—	—	cf.
V. wingei	◑	—	—	—	—	—	—	—	—	—	×
V. sp. 1	◑	—	—	—	—	—	—	—	—	—	×
Nannopithex quaylei	○	×	—	—	—	—	—	—	—	—	—
N. sp. 1	○	×	—	—	—	—	—	—	—	—	—
Pseudoloris crusafonti	○	cf.	—	×	—	—	—	—	—	—	—
P. parvulus	◑	—	—	—	—	—	—	—	—	—	×
Necrolemur zitteli	◑	—	—	×	—	—	—	—	—	×	×
Microchoerus sp. (Grisolles)	○	—	—	×	—	—	—	—	—	—	—
M. wardi	○	×	—	—	—	—	—	—	—	—	—
M. creechbarrowensis	○	×	—	—	—	—	—	—	—	—	—
Europolemur collinsonae	○	×	—	—	—	—	—	—	—	—	—
Leptadapis magnus	◑?	aff.	—	—	—	—	—	—	—	—	—
Adapis sudrei	○	—	—	cf.	—	—	—	—	—	×	—
?A. laharpei	○	—	—	—	—	—	×	—	—	—	—
Plesiarctomys curranti	○	×	—	—	—	—	(cf.)	—	—	—	—
P. hurzeleri	○	×	—	—	—	—	(×)	×	—	×	—
Ailuravus stehlinschaubi	○	×	—	—	—	—	×	—	—	—	—
Gliravus robiacensis	◑ aff.	—	—	aff.	—	—	—	—	—	×	×
Sciuroides rissonei	○	×	—	—	—	—	—	—	—	—	—
S. russelli	○	—	—	×	—	—	—	—	—	—	—
S. siderolithicus	○	—	—	—	—	—	×	—	—	×	×
Treposciurus helveticus preecei	○	×	—	—	—	—	—	—	—	—	—
Suevosciurus authodon	○	×	—	—	—	—	—	—	—	—	—
Paradelomys crusafonti	◑	—	—	cf.	—	—	—	—	—	cf.	cf.
Elfomys tobieni	◑	—	—	—	—	—	—	—	—	×	—
Pseudoltinomys mamertensis	◑	—	—	?	—	—	—	—	—	—	aff.
Theridomys varleti	○	—	—	×	—	—	—	—	—	—	—
Remys minimus	○	—	—	—	—	—	—	—	—	×	cf.
Heterohyus sudrei	◑	cf.	—	×	—	—	—	—	—	×	—
H. nanus	◑	aff.	—	—	—	—	—	—	—	×	—
H. morinionensis	○	×	—	—	—	—	—	—	—	—	—
Cynohyaenodon cayluxi	○	—	—	—	—	—	—	—	—	—	×
Hyaenodon heberti	◑	—	—	—	—	—	—	—	—	aff.	—
Simamphicyon helveticus	○	—	—	—	—	—	×	—	—	×	×
Quercygale angustidens	◑	—	—	—	—	—	×	—	—	×	×
Vulpavoides cooperi	○	×	—	—	—	—	—	—	—	—	—
Propalaeotherium parvulum	◐	aff.	—	—	—	—	aff.	—	—	—	cf.
Lophiotherium siderolithicum	○	×	—	—	—	—	×	—	—	×	—
Anchilophus desmarestii	cf.◐	—	—	—	×	—	(×)	—	—	cf.	×
A. gaudini	◑ cf.	—	—	—	—	—	×	cf.	—	cf.	×
A. dumasii	◑	—	—	—	—	—	×	—	—	cf.	cf.

Table 38 (*continued*)

	Range	Creechbarrow	Barton C–F	Grisolles	Paris	Sergy	Eclépens-Gare	Le Castrais	La Guittardie	Robiac	Le Bretou
A. depereti	◐	–	–	–	–	–	–	cf.	–	cf?	–
Plagiolophus curtisi curtisi	○	–	×	–	–	–	–	–	–	–	–
P. curtisi creechensis	○	×	–	–	–	–	–	–	–	–	–
P. cartailhaci	○	–	–	–	–	–	–	×	–	×	–
P. annectens	◑	–	–	–	–	–	aff.	aff.	–	aff.	aff.
Leptolophus nouleti	○	–	–	–	–	–	–	×	–	–	–
L. stehlini	○	–	–	–	–	–	(×)	×	–	×	–
Palaeotherium ruetimeyeri	◐	–	–	–	–	–	–	–	–	aff.	–
P. pomeli	○	–	–	–	–	–	–	×	×	×	–
P. castrense castrense	◐	–	–	–	–	–	–	×	–	–	–
P. c. robiacense	○	–	–	–	×	–	–	–	×	×	–
P. siderolithicum	◑	–	–	–	–	–	×	×	–	×	cf.
P. lautricense	○	–	–	–	–	–	cf.	×	–	–	–
P. muehlbergi	◑	–	?aff.	–	–	–	–	–	–	–	–
Lophiodon lautricense	○	–	–	–	cf.	–	×	×	–	×	–
L. thomasi	○	–	–	–	–	×	–	–	–	–	–
L. tapiroides	◐	–	–	–	–	–	×	–	–	–	–
Chasmotherium cartieri	◐	–	–	–	–	–	×	–	–	×	–
Cebochoerus minor	◑	–	×	–	–	–	×	×	–	–	?
C. robiacensis	○	×	–	–	–	–	–	×	–	×	–
Acotherulum campichii	○	×	–	×	–	–	×	–	–	×	–
Mixtotherium gresslyi	● aff.	aff.	–	–	–	–	aff.	–	–	–	–
M. infans	◐	–	–	–	–	–	cf.	–	–	–	–
Haplobunodon venatorum	○	×	–	–	–	–	aff.	–	–	–	–
Anthracobunodon louisi	○	–	–	×	–	–	–	–	–	–	–
Choeropotamus lautricensis	○	–	–	–	–	–	–	×	–	×	–
Dacrytherium elegans	◑	×	–	–	–	–	×	–	–	–	aff.
Catodontherium robiacense	○	–	–	–	–	–	×	–	–	×	–
C. ?paquieri	○	–	–	–	–	–	–	×	–	–	–
Leptotheridium lugeoni	◑	–	–	–	–	–	×	–	–	–	–
L. traguloides	◐	–	–	–	–	–	–	–	–	cf.	aff.
Tapirulus schlosseri	◑?	–	–	–	–	–	×	–	–	×	×
Robiacina minuta	○	–	–	–	–	–	–	–	–	×	×
R. weidmanni	○	–	–	–	–	–	×	–	–	–	–
Xiphodon castrense	○	–	–	–	–	–	×	×	–	×	×
Paraxiphodon cournovense	○	–	–	–	–	–	–	–	–	×	–
Haplomeryx picteti	○	–	–	–	–	–	×	–	–	×	×
Dichodon cervinus	◑	cf.	–	–	–	–	cf?	–	–	–	–
D. subtilis	○	–	–	–	–	–	×	–	–	–	–
Pseudamphimeryx pavloviae	◑	–	–	–	–	–	–	–	–	×	×
P. renevieri	◑	–	–	–	–	–	×	–	–	aff.	–
P. valdensis	○	–	–	–	–	–	×	–	–	–	–

iii. Discussion. An attempt has been made in each zone to find the same genera represented by different species, and use them as zonal indices, with varying degrees of success. In some cases it is thought that the species represent stages in evolutionary sequences – e.g. *Lophiotherium pygmaeum* to *L. siderolithicum* (see Savage *et al.* 1965, and herein); *Palaeotherium eocaenum* to *P. lautricense* (see Franzen 1968); and *Haplobunodon solodurense* to *H. venatorum* (p. 409). In the former case, transitional 'advanced' forms of *L. pygmaeum* occur at Egerkingen *β* (see

Stehlin 1905*b*). In the case of *Ailuravus stehlinschaubi* and *Lophiodon thomasi* the probable ancestral species (*A. picteti* and *L. cuvieri*) occur in the *eocaenum–rhinocerodes* Zone, but also range down into earlier Lutetian strata. Three of the *lautricense–siderolithicum* Zone index species (*L. siderolithicum*, *Acotherulum campichii* and *Plesiarctomys hurzeleri*) also have probable descendant species (*L. cervulum*, *A. saturninum* and *P. gervaisii*) in Ludian strata. In the former case, the Alès Basin has yielded a series of transitional forms from the Fons localities, linking *L. siderolithicum* from Robiac to *L. cervulum* from Euzet (Remy 1967, Garimond *et al.* 1975). The species *Lophiodon lautricense*, *Chasmotherium cartieri*, *Leptolophus stehlini* and *Ailuravus stehlinschaubi* last occur at the top of the *lautricense–siderolithicum* Zone, marking also the last appearance of the family Lophiodontidae, the family Helaletidae in Europe, the genus *Leptolophus* and the subfamily Ailuravinae in the stratigraphic record.

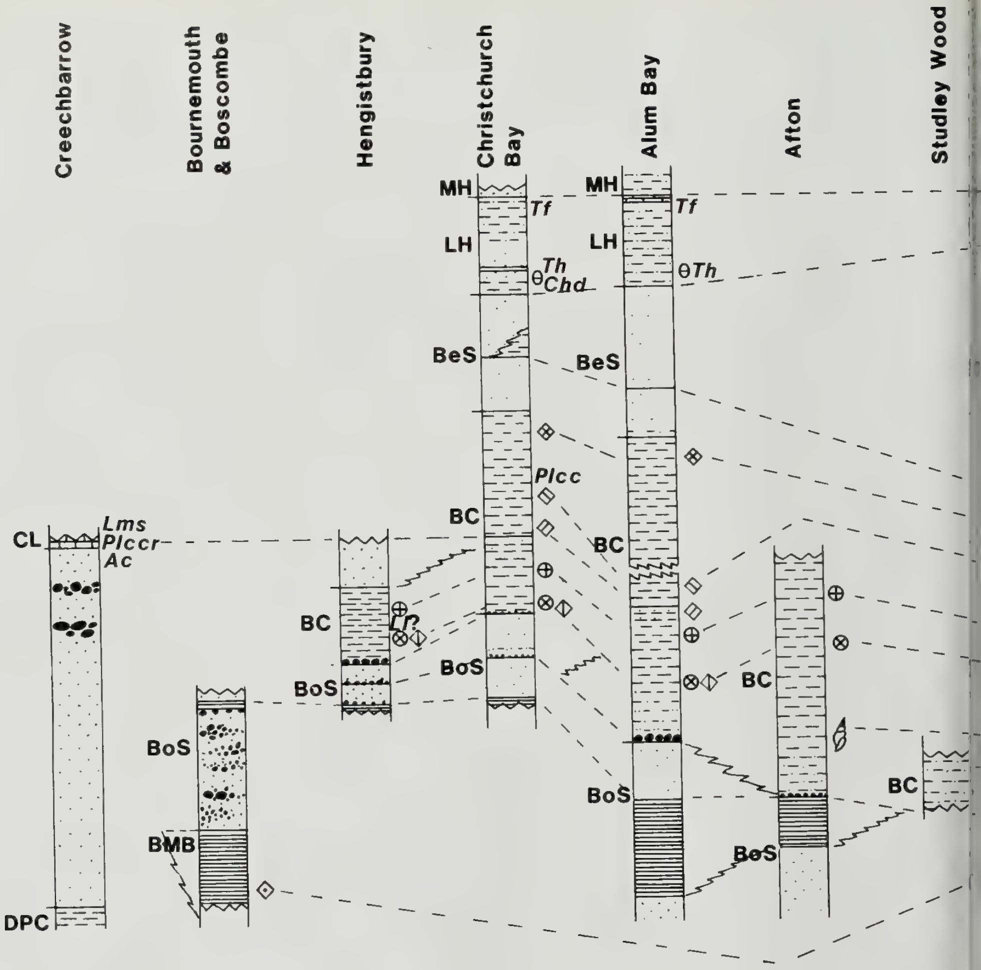
The principal and most widespread taxa as well as those forming stratigraphical morphoclines have been chosen to define the two zones erected here. Numerous other lesser-known taxa with assumed similar evolutionary relationships occur through this period of time.

iv. Further subdivision by mammalian biostratigraphy. It is difficult to locate the Lutetian–Auversian boundary within the *eocaenum–rhinocerodes* Zone. Changes from one fauna to another in the Egerkingen fissures are highly relevant to this problem but the stratigraphical order of these fissures is unknown, being postulated on evolutionary grade. It is probable that Egerkingen β is the most recent; Egerkingen α appears more advanced than Egerkingen γ but less so than Egerkingen β (see Hartenberger 1972). It is possible that with the probable chronological range involved these fissures straddle the Lutetian–Auversian boundary. A study in progress on early species of *Plagiolophus* may cast further light on this problem.

Detailed correlation between the Hampshire and Paris basins has already been shown to be a problem and has ramifications in any attempt to arrange the various Bartonian mammal localities in succession. Text-fig. 67, however, attempts this by piecing together the various partial correlations which have been made using different groups of organisms.

Hartenberger & Louis (1976) placed the mammal fauna of Grisolles, which occurred in about the middle of the Calcaire de St Ouen in the east of the Paris Basin, later than Robiac and earlier than Fons 4 in the scale of niveaux-repères, all three being included in the Marinesian. This contrasts with most authors who place Fons 4 near the base of the Ludian (e.g. Garimond *et al.* 1975) and is contrary to evidence from the charophytes (Grambast 1962, 1964, 1972), which correlates Robiac with higher, not lower, parts of the Calcaire de St Ouen. Moreover, Grisolles contains a number of species typical of the *lautricense–siderolithicum* Zone but which do not occur in strata immediately overlying those from which the Robiac fauna has been obtained (Garimond *et al.* 1975): i.e. *Pseudoloris crusafonti*, *Adapis* cf. *sudrei* and *Acotherulum campichii*. The rest of the fauna too is very different from those of Fons 1, 2, 5, 6 and 7, and also from Le Bretou (except for some long-ranging species), which occupy Hartenberger & Louis' (1976) postulated level for Grisolles in the Alès Basin (see Sigé 1976, Sudre 1978*b*, Louis & Sudre 1975, Crochet 1979, 1980 and Crochet *et al.* 1981 for faunal details). Grisolles, which is demonstrably well within the Bartonian, is therefore considered to be earlier than Robiac which is dated as late Marinesian because of its position immediately below the *L. lautricense–L. stehlini* extinction datum.

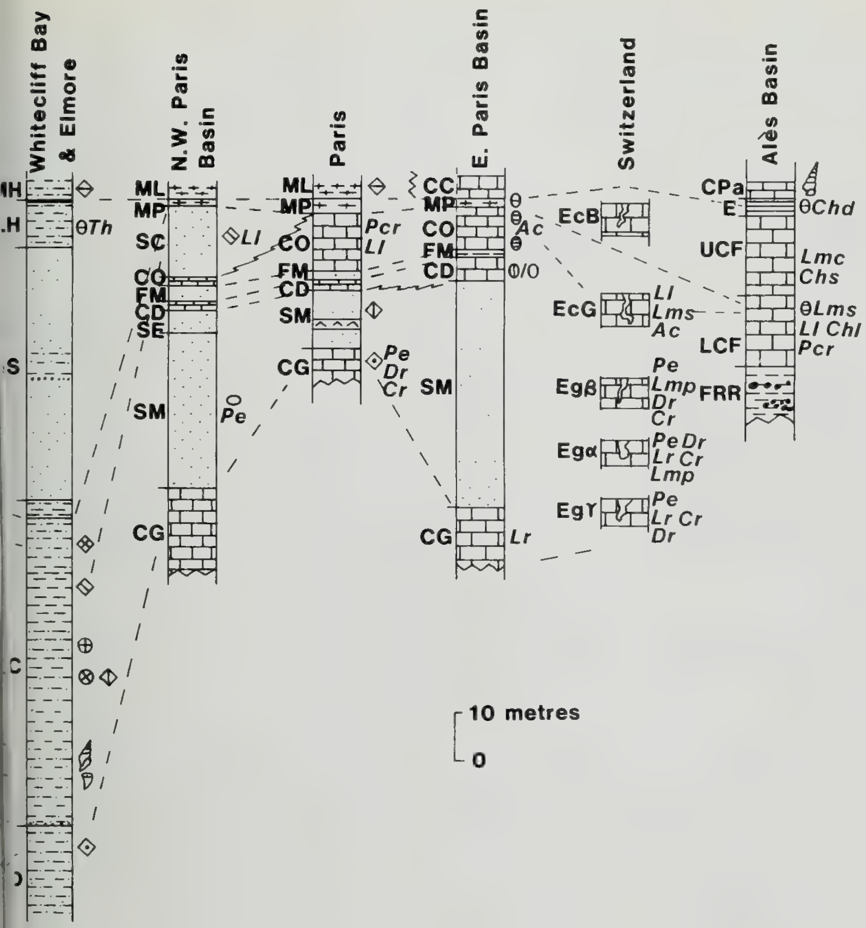
The reasons given by Hartenberger & Louis (1976) for their dating of Grisolles relative to strata in the Alès Basin was based on evolutionary grade in certain rodents. The arguments ran thus: 1, *Theridomys varleti* and *Pseudoltinomys* sp. are more primitive than *T. euzetensis* and *P. mamertensis* from Fons 4; 2, the *Pseudoltinomys* is very similar to that from Le Bretou, a fissure locality considered slightly younger than Robiac; and 3, *Suevosciurus russelli* and *Gliravus* aff. *robiacensis* are more advanced than *S. romani* and *Gliravus robiacensis* from Robiac. The *Pseudoltinomys* by their own admission is very poorly known; the intrageneric relationships of *Suevosciurus russelli* (shown on p. 300 to belong to *Sciuroides*) with *S. romani* (synonymized with *Sciuroides siderolithicus*, p. 300) are obscure; it seems likely that *S. siderolithicus* gave rise to *S. ehrensteinensis* via transitional forms recorded at Weidenstetten (Schmidt-Kittler 1971*a*) and Eclépens B, whereas *S. russelli* is closer to *S. rissonei*, which occurs at Creechbarrow



Text-figure 67 Correlation of European Bartonian strata. Stratigraphical columns range into strata higher and lower than Bartonian in most cases. For key to lithological symbols, see Text-fig. 2, p. 201. Abbreviations of lithostratigraphy are given on left of columns and abbreviations (mammals) and symbols (other biota) of biostratigraphy are given on right of columns. Jagged break in Alum Bay column indicates the omission of *c.* 9m of Barton Clay.

Abbreviations of lithostratigraphy: BC = Barton Clay Formation; BeS = Becton Sand Formation; BMB = Bournemouth Marine Beds; BoS = Boscombe Sands; CC = Calcaire de Champigny; CD = Calcaire de Ducy; CG = Calcaire Grossier; CL = Creechbarrow Limestone Formation; CO = Calcaire de St Ouen; CPa = Calcaire à *Potamides aporoschema*; DPC = Dorset pipe clays; E = marnes d'Euzet; EcB = Eclépens B; EcG = Eclépens-Gare; Eg = Egerkingen; FM = Formation de Mortefontaine; FRR = formation rouge de Robiac; LCF = lower Calcaire de Fons; LH = Lower Headon Beds; MH = Middle Headon Beds; ML = Marnes à *Lucina inornata*; MP = Marnes à *Pholadomya ludensis*; SC = Sables de Cresnes; SD = Selsey division; SE = Sables d'Ezanville; SM = Sables Moyens; UCF = upper Calcaire de Fons.

associated with a typical *lautricense–siderolithicum* Zone fauna. This leaves only the *Gliravus* at Grisolles supporting a younger age than Robiac. The coefficients of variation given by Hartenberger & Louis (1976: 89, tab. 4) for the lengths of upper and lower preultimate molars of *Gliravus* aff. *robiacensis* from Grisolles exceed 9, which is a good indication that more than one species is represented. In view of these problems, it is considered that more confidence can be


Whitecliff Bay & Elmore
N.W. Paris Basin
Paris
E. Paris Basin
Switzerland
Alès Basin
HH
H
S
C
θTh
ML
MP
SC
CO
FM
CD
SE
SM
CG
Pe
LI
Pcr
CC
θ/0
Ac
Lr
EcB
EcG
Egβ
Egα
Egγ
Lms
Lmp
Dr
Cr
CPa
E
UCF
LCF
FRR
θChd
Lmc
Chs
θLms
LI Chl
10 metres
0

Text-figure 67, continued. Abbreviations of mammal taxa: *Ac* = *Acotherulum campichii*; *Cr* = *Cebochoerus ruetimeyeri*; *Chd* = *Choeropotamus depereti*; *Chl* = *C. lautricensis*; *Chs* = *C. sudrei*; *Dr* = *Dichobune robertiana*; *Ll* = *Lophiodon lautricense*; *Lr* = *L. rhinocerodes*; *Lmc* = *Lophiotherium cervulum*; *Lmp* = *L. pygmaeum*; *Lms* = *L. siderolithicum*; *Pcr* = *Palaeotherium castrense robiacense*; *Pe* = *P. eocaenum*; *Plcc* = *Plagiolophus curtisi curtisi*; *Plccr* = *P. curtisi creechensis*; *Tf* = *Thalerimys fordi*; *Th* = *T. headonensis*.

Biotic symbols: Dinocysts: ◈ = first occurrence of *Areoligera undulata* and *Areosphaeridium multicornutum*: ⟠ = first occurrence of *Rhombodinium draco*; ◇ = base zone BAR-2 of Bujak *et al.* (1980); ◊ = first occurrence of *R. porosum*; ❖ = base zone BAR-4; ⬖ = first occurrence of *Homotryblium floripes* and *Kisselovia clathrata angulosa.* Charophytes: ○ = zone of Nogent-l'Artaud; Φ = zone of Chéry-Chartreuve; θ = zone of St Ouen; θ = zone of Robiac; θ = zone of Verzenay (base). *Nummulites*: ⊗ = *N. prestwichianus*; ⊕ = *N. rectus* first appearance. Coral: ∇ = *Paracyathus*. Gastropods: ∆ = *Ectinochilus planum*; ∆ = *Potamides aporoschema*. Ostracod: ⬭ = *Cytheretta cellulosa*.

Sources: Bosma (1974), Bujak *et al.* (1980), Châteauneuf (1980), Costa *et al.* (1976), Curry (1942, 1977), Depéret (1910), Ginsburg *et al.* (1965, 1977), Grambast (1962, 1964, 1972), Keen (1978), Kemp *et al.* (1979), Lemoine & Abrard (1926), Louis & Sudre (1975), Roman (1904), Stehlin (1903, 1904*b*, 1905*b*, 1906, 1908, 1918), Sudre (1969*a*, 1978*b*).

attached to other elements in the mammal fauna and to the charophytes than to rather generalized ideas of evolutionary grade in those rodent species whose exact relationships are still unclear.

Mammals recorded from other Calcaire de St Ouen localities include *Palaeotherium castrense robiacense* Franzen 1968 from about the middle of the formation in Paris (Lemoine & Abrard 1926). This subspecies is recorded from the top of the *lautricense–siderolithicum* Zone at Robiac, associated with the Robiac charophyte zone. Fossils characterizing the latter zone are recorded from immediately below the Marnes à *Pholadomya ludensis* in the northern Paris Basin, thought to be equivalent to the Sables de Monceau in the region of Paris (Cavelier 1979: 157). *P. c. robiacense* appears thus to occur at a lower horizon here, but the problems posed for correlation within the Paris Basin by the condensed sequences and the lateral facies changes near the basin margins make this by no means the only interpretation. The relationship to Grisolles, also occurring at about the middle of the formation, is equally a problem, especially as there is no mammalian faunal overlap between the two localities.

In England, only two taxa are common to the Creechbarrow Limestone and the Barton Clay: Microchiroptera gen. et sp. indet. 1 (p. 241) and *Plagiolophus curtisi* (p. 353). The slight differences of size and morphology between the two assemblages of the latter have resulted in two subspecies being described. On the theoretical concept of evolutionary grade, *P. curtisi creechensis* from Creechbarrow is considered slightly more primitive than *P. curtisi curtisi* from Barton bed D/E, and therefore slightly earlier. Creechbarrow and Grisolles share only two short-ranged species: *Pseudoloris crusafonti* (cf. determination at Creechbarrow) and *Acotherulum campichii*. Ideas of evolutionary grade in two other genera give contradictory results: Creechbarrow *Sciuroides rissonei* appears in some respects to be more primitive than Grisolles *S. russelli*, whereas the Grisolles *Microchoerus* is more primitive than and intermediate in size between Creechbarrow *M. wardi* and *M. creechbarrowensis*. The choice is difficult but the evidence from *Microchoerus* is more convincing as it fits better with the subsequent sequence of events in *Microchoerus* evolution; in contrast, the relationships of *S. russelli* are more obscure. Grisolles is thus tentatively considered to be slightly earlier than Creechbarrow, which in this case must be Marinesian rather than late Auversian.

The various mammaliferous localities of the Castrais region of the Aquitaine Basin (Sables du Castrais) are thought to vary somewhat in age (see Richard 1946 for faunal lists; Sudre 1969*a*). They were considered by Remy (1965) to be earlier than Robiac because they contained a lower-crowned and therefore more primitive species of *Leptolophus*, *L. nouleti* (Stehlin 1904*a*) Remy 1965, than at Robiac (*L. stehlini*). Increase in crown height is almost universally considered to be an advancement, but at other localities in Le Castrais *L. stehlini* also occurs. It is most likely that the latter are younger than the localities yielding *L. nouleti*. Castrais *L. stehlini*, moreover, has slightly lower crown height than Robiac *L. stehlini*, although the difference is not nearly so marked as with *L. nouleti*. *L. stehlini* from Mormont (Eclépens A and probably, although not labelled, Eclépens-Gare) is very similar in crown height to that of Le Castrais, suggesting close correlation. An $M_{1/2}$ from the Auversian of Le Guépelle was recorded as '*Plagiolophus* taille de *P. annectens*' by Ginsburg *et al.* (1965). It more closely resembles *Leptolophus* in morphology and is at least as low-crowned as *L. nouleti*. It is thus possible that the Castrais localities with *L. nouleti* are as old as Auversian.

Other elements in the Castrais and Eclépens-Gare faunas have been shown to be slightly different from those of Robiac, indicating that they are probably slightly older (e.g. Sudre 1969*a*; Franzen 1968), but relationships with localities such as Creechbarrow and Grisolles are less easy to envisage. Creechbarrow and Eclépens-Gare share a number of short-ranged species (viz. *Lophiotherium siderolithicum*, *Haplobunodon venatorum* and *Ailuravus stehlinschaubi*), but there are subtle differences in these, e.g. in size, which could just as easily result from geographical as from stratigraphical distance. The possibility of Creechbarrow *Sciuroides rissonei* being the ancestor of Eclépens-Gare *S. siderolithicus* suggests that Creechbarrow is earlier than Eclépens-Gare.

Le Bretou has been considered to be slightly younger than Robiac but still Bartonian, on the basis of the occurrence of *Remys minimus*, *Robiacina minuta*, *Xiphodon castrense* and *Simamphicyon helveticus* (Hartenberger *et al.* 1974; Sudre 1978*b*: 185). This is also supported by the presence of *Sciuroides siderolithicus*, probably that recorded as *Suevosciurus* (*Treposciurus*) *mutabilis* by Hartenberger (1973: 65) and as *Suevosciurus* cf. *romani* by Hartenberger *et al.* (1974).

Below is the suggested succession of European Bartonian mammal localities. It conforms with correlation based on other groups.

England	*Paris Basin*	*Switzerland*	*S. France*
			Le Bretou
	Paris?		Robiac
Barton C–F	Berville	Eclépens-Gare	Le Castrais (Lautrec etc.)
Creechbarrow	Paris?		
	Grisolles		
Hengistbury	Sergy/Latilly?		
		Egerkingen β?	Le Castrais (Viviers)?
	Le Guépelle/ Arcis-le-P.	Egerkingen α?	Lissieu?

The solid line indicates the boundary of the two zones and the dashed line the Auversian–Marinesian boundary. The '?' indicates doubt regarding position and, in the case of Paris, two possible positions for the Calcaire de St Ouen specimens are suggested. Other localities like La Livinière in southern France and Laguarrès in Spain are thought to be early Bartonian but have so far yielded sparse mammal faunas, or only endemic taxa or those which are not distinctive of age (see Hartenberger 1973: 67 for lists). *Lophiodon rhinocerodes* and *Palaeotherium r. ruetimeyeri* have recently been recorded from the Grès de Brenne at Fonliasmes, near Poitiers, France (Brunet & Gabilly 1981) and attributed an Auversian age. The two taxa certainly correspond to the *eocaenum–rhinocerodes* Zone but could be either late Lutetian or Auversian.

It is worth noting that the junction of the two mammal zones must be close to the base of the *Rhombodinium draco* dinocyst zone and thus the mammal evidence supports Curry's (1981) proposed modification of the base of the Bartonian.

Evidence from Hampshire Basin sedimentation

West of Whitecliff Bay, the beginning of a series of facies changes from predominantly argillaceous to predominantly arenaceous strata of less marine aspect affects most of the post-London Clay and pre-Fluviomarine strata. The result is that most fossils disappear and dating the western sequences is difficult. At intermediate localities such as Afton, Alum Bay, Barton Cliff and Bournemouth, thinning, facies interdigitation and the persistence of some groups of organisms (e.g. dinocysts) as far west as Bournemouth allows some dating of problem strata from the late Lutetian into the Bartonian (Eaton 1976; Costa *et al.* 1976).

Actual facies change trends are observable at Hengistbury where there is an increase in sand content and abundance of pebble stringers in a westerly direction along the section in the Barton Clay ('Hengistbury Beds') (Hooker 1975). Fisher (1862: 86–88) noted an increase in abundance of pebbles westwards in the basal pebble bed of the Barton Clay at High Cliff, and (1862: 89, figs 3–4) suggested correlation of what is now referred to the upper part of the Boscombe Sands at High Cliff with what is herein referred to lower parts of the Barton Clay Formation in Alum Bay.

Curry (1977), from recognition of two nummulite horizons in the lower Barton Clay (as 'Hengistbury Beds'), correlated an overlying sand at Hengistbury with Bed A3 (High Cliff Sands and Clays of Wright, 1851) at High Cliff and Barton Cliff.

Because of the interruption in the coastal exposure at Poole harbour west of Bournemouth, combined with more facies change and reduction in fossil content, the Creechbarrow sequence is very difficult to match with those further east. The only key seems to be the giant flints which occur at various horizons from *c.* 7 m below the Creechbarrow Limestone downwards. Flints of comparable size are recorded from the Boscombe Sands of Bournemouth (Gardner 1879: 218; Prestwich 1849: 46–47), the slightly diachronous basal Barton Clay pebble/cobble beds at Hengistbury and Alum Bay. They thus appear to occupy a relatively narrow span of strata east of Poole Harbour and it is logical to suggest that they do the same at Creechbarrow. If the Creechbarrow Limestone represents the end of a regression like similar limestones in the later Fluvio-marine series then the stratigraphically closest regression in the marine sequence, sandwiched between the Boscombe Sands and Barton Clay Bed D (from faunal evidence; see Text-fig. 67, pp. 246–7) is that of Barton Clay Bed A3. If the progressive reduction of clastic sediment in the Creechbarrow sequence as the limestone is reached represents a raising of the water table resulting from a transgression, then a correlation with Barton Clay Bed B (the nearest transgressive stratum) might be more appropriate.

Palaeoenvironments, palaeoecology and palaeogeography

Depositional environments

The marine province. The Barton Clay and Becton Sand Formations in Christchurch Bay have been shown in the stratigraphical section, pp. 197–212, to have been deposited in a series of three cycles. The erosive base of each cycle is taken to indicate the rapid transgression of a shelf sea, followed by a gradual regressive (progradational) phase, ending in shoreface sands.

At the western end of Christchurch Bay at Friar's Cliff and Hengistbury, there is evidence in lower parts of the sequence of two more cycles. These occur in the upper part of the Boscombe Sands, which here underlie the Barton Clay Formation.

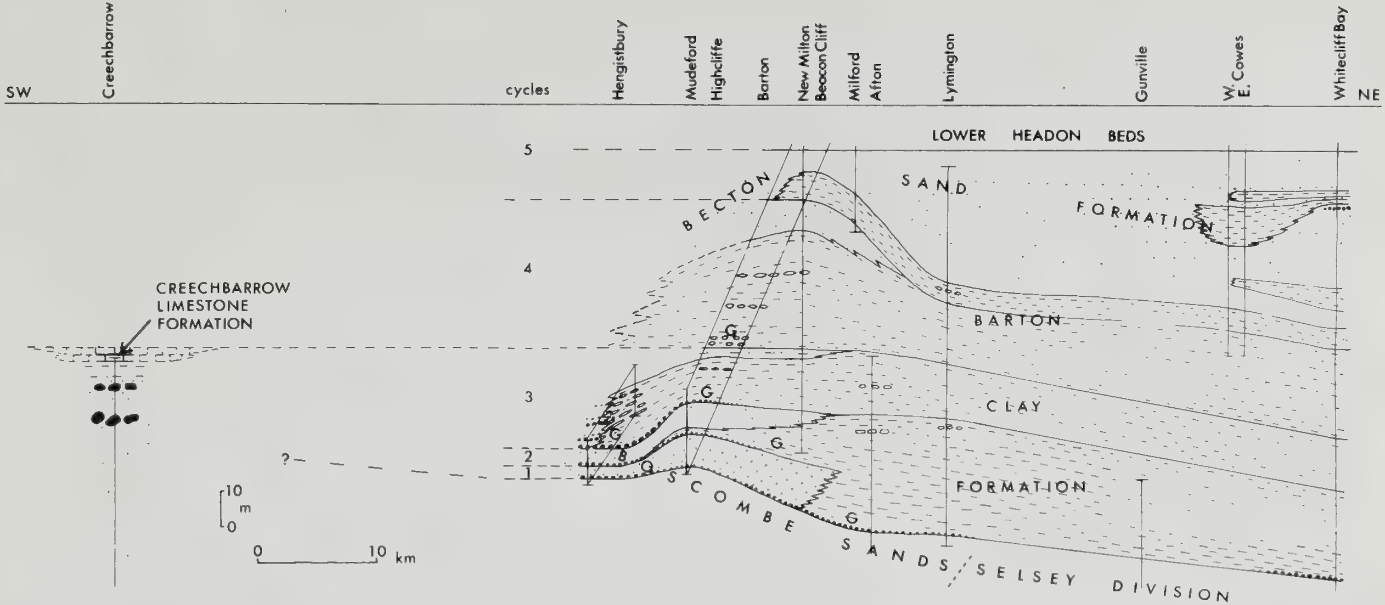
The upper of these cycles has a basal pebble bed and passes from non-glauconitic clayey sand to non-glauconitic sand, both with *Ophiomorpha* and plant debris. At Hengistbury this cycle spans Boscome Sands beds 2 and 3 (Hooker 1975: fig. 3). At Friar's Cliff it spans the 'Highcliff Sands' of Gardner from the pebble bed upwards (see Hooker 1975: fig. 2) or beds 2 and 3 of Fisher (1862: 87, fig. 2).

The lower of these cycles at Hengistbury has a basal pebble bed, resting on laminated lignitic clays and consists almost entirely of light non-glauconitic sand with *Ophiomorpha*, with an impersistent seam of pipe-clay at the top (Boscombe Sands bed 1 of Hooker, 1975: fig. 3; the underlying '?Bournemouth Marine Beds' were incorrectly identified). Only the upper part of this cycle is exposed at Friar's Cliff, where it consists of a thicker unit of light-coloured sands ('Highcliff Sands' of Gardner below the lower pebble bed shown in Hooker 1975: fig. 2). The equivalent in Alum Bay is considered to be the sands of bed 28 of Prestwich (1846).

When traced eastwards these sandy units successively pass laterally into glauconitic sandy silts and silty clays of lower parts of the Barton Clay Formation (Huntingbridge division, including Elmore Member in part). The latter at Afton and Whitecliff Bay seem to continue up into time-equivalents of the lower part of the lower cycle of the Barton Clay in Christchurch Bay, entirely within Elmore facies. They cannot here be subdivided into cycles. These recognition problems are likely to be because successive cycles, up to the lower one of the Barton Clay in Christchurch Bay, transgress each other. The progradational (regressive) phases of the first two did not develop seaward sufficiently to cause facies changes in the more offshore sequence further east (e.g. Afton and Whitecliff Bay). The cycles will here be numbered 1 to 5. The lower, middle and upper of the Barton Clay and Becton Sand Formations in Christchurch Bay, described on pp. 206–7, are numbered 3, 4 and 5 respectively. The lower and upper of the upper part of the Boscombe Sands are numbered 1 and 2 respectively. See Text-fig. 68 for the model.

The glauconitic facies of the cycles are best developed in the west of the area (Christchurch Bay, Alum Bay). Glauconite is considered to form in the sea under conditions of some turbulence, with low sedimentation rates and some organic matter (Reineck & Singh 1980: 151). Porrenga (1967) noted that it was being formed today in the tropics at depths of 125–250 m, controlled by temperature (10°–15°C). However, Bell & Goodell (1967) recorded authigenic glauconite in shelf environments at various latitudes, ranging in depth from 20–1780 fathoms (= 37–3255 m), being formed often inside foraminiferid shells or replacing coprolites or mica flakes; they found that it tends to form in a band parallel to the coastline.

Murray & Wright (1974: 50–51), on the basis of foraminiferids, considered beds B–E at Barton Cliff (glauconitic beds of cycle 4) to have formed under water 50–100 m deep, and beds A2 and F–lower H (non-glauconitic clays of cycles 3 and 4) no deeper than 50 m. Lower and higher strata were referred to an intertidal or estuarine environment and they concluded that 'the Barton Beds at their type locality represent a full marine cycle from continental deposits,


SW
Creechbarrow
cycles
Hengistbury
Mudeford
Highcliffe
Barton
New Milton
Beacon Cliff
Milford
Afton
Lymington
Gunville
W. E. Cowes
Whitecliff Bay
NE
LOWER HEADON BEDS
5
4
3
2
1
?
CREECHBARROW LIMESTONE FORMATION
BECTON SAND FORMATION
BARTON CLAY FORMATION
SCOMBE SANDS
SELSEY DIVISION
G
Q
B
10 m 0
0 10 km

Text-figure 68 Somewhat schematic slice section of Hampshire Basin Bartonian strata, trending approximately north-east/south-west, to show facies distributions and cycles. Vertical bars or oblique windows indicate extent of recorded strata at a given locality. Where present the base of the Lower Headon Beds has been used as the top horizontal datum. For key to lithological symbols, see Text-fig. 2, p. 201. Sources of data: Curry (1942), Hooker (1975), Prestwich (1846) and Whitaker (1910, 1917).

through marsh, inshore and offshore shelf, and back to shallow water conditions'. The close lithological, and to an extent faunal, similarities between cycles 3 and 4 suggest that their 'full marine cycle' may have been repeated. The uniqueness of their agglutinated foraminiferal fauna from A1 (suggesting to them hyposaline tidal marsh) by their own admission takes no account of either the absence by leaching of calcareous fossils in this bed, or the probable absence of agglutinated forms from glauconitic beds in cycle 4 by disintegration on burial (Murray & Wright 1974: 48, 50). See also comments by Curry (1977: 404).

Burton (1933) noticed that certain molluscs occurred in the Lower and Upper Barton Beds, but not in the Middle. These are in fact almost entirely restricted to the sands and clayey sands of Beds A3 and H and thus predominate at homologous stages in cycles 3 and 4. Representative species are: *Vepricardium porulosum*, *Glans oblonga*, *Calliostoma nodulosum*, *Homalaxis* sp., *Cordieria semicostata* and *Tornatellaea simulata*. The very rare brachiopod *Argyrotheca piperipyxis* has a similar distribution. The gastropod genus *Terebellum* also has a similar occurrence but is represented by different species (*T. fusiforme* in A3; *T. sopitum* in upper H). Further repetitions occur between the sandy parts of cycles 4 and 5, e.g. *Glans oblonga* at Barton. Further east this extends also to *Chama squamosa*, *Vepricardium porulosum*, *Crassatella tenuisulcata* and *Terebellum sopitum*, which occur in cycle 5 in Whitecliff Bay. This list is from Gardner *et al.* (1888: 605) who called the horizon at Whitecliff Bay the 'Chama Bed', but according to the dinocysts (Bujak *et al.* 1980) and the lithostratigraphy it belongs to cycle 5. The true Chama Bed of Wright (1851) at Barton belongs to cycle 4.

There are conflicting ideas on water depth in lower parts of the sequence in the east of the area. Murray & Wright (1974: 21) could find no foraminiferans in most of the weathered, poorly-exposed cliff section in Whitecliff Bay and, from the descriptions of the succession by Gardner *et al.* (1888) and White (1921*a*), concluded that clays above the *N. prestwichianus* bed represented 'a return to intertidal, fluvial marsh, and channel environments'. This interpretation is not corroborated by the fully marine mollusc faunas from the 'Chama Bed' (Gardner *et al.* 1888) or in blue clays with *N. rectus* (personal observation). Likewise, the Elmore Member (Fisher beds XVIII–lower XIX) was considered to be intertidal (Murray & Wright 1974: 21), whereas an almost identical lithology (beds S–W) at Fawley (Curry *et al.* 1968: 195) was considered to have accumulated in deeper water than had the Selsey division (beds B–R) and under low oxygenation conditions with limited current movement, which were unfavourable to a rich benthos, in particular molluscs.

It is probable that cycles 3 and 4 represent upward shallowing sequences from richly (more onshore shelf) or poorly (more offshore shelf) glauconitic greenish clays and silts (50–100 m depth) through non-glauconitic blue or grey clays (maximum 50 m depth) to (in the west only) lower shoreface sands (with *Solen*, *Panopea*, *Pinna*, see Curry 1977, and possibly *Ophiomorpha* in cycle 3). Cycle 5 represents a similar upward shallowing sequence but from non-glauconitic clays (*c.* 50 m depth?) through shoreface sands to shelly storm washover sands (at Barton Cliff, Plint 1984). Both molluscs (Gardner *et al.* 1888: 592) and foraminiferans (Murray & Wright 1974) in the upper sandy part of the clays indicate the beginning of a major salinity reduction towards the brackish and freshwater environment of the overlying Lower Headon Beds which conclude cycle 5. At this same lithological horizon in Whitecliff Bay, however, the salinity appears to have been more normally marine with the 'Chama bed' type fauna mentioned above.

At Barton Cliff archaeocetes are known from both the glauconitic and non-glauconitic clay facies and these presumably lived or at least died in this environment. The few land mammals are mainly medium- to large-sized, probably a feature of collecting availability and bias; the bat (p. 242) is an unusual exception, found admittedly by sieving techniques, this group being very rare in marine sediments and rare even at Creechbarrow. The skull of *Plagiolophus curtisi* is unusual in having the cranium and mandible in association, indicating a fairly nearshore site of deposition.

The non-marine province. Knowledge of this province is restricted to strata on Creechbarrow Hill. The sands, clays and conglomerates beneath the Creechbarrow Limestone Formation are poorly exposed and little knowledge has been gained of sedimentary structure. Nevertheless the poor sorting, the occasional conglomeratic horizons, and the unrolled state of the flints (indicating a nearby source) all suggest that they may be distal alluvial fan deposits (see Blissenbach 1954, Hooke 1967, Reineck & Singh 1980).

A different and more complex depositional interpretation is required to account for the various features of the Creechbarrow Limestone. Indications of three different environments have been found:

1. Fluvial:
   - a. abundant quartz grains in an otherwise fine-grained limestone;
   - b. terrestrial mammal remains showing evidence of water transport (see below);
2. Lacustrine:
   - a. freshwater gastropod molluscs;
   - b. cyanophyte algal oncoliths often with laminae thin on one side;
   - c. calcareous ?chironomid tubes associated with the algae;

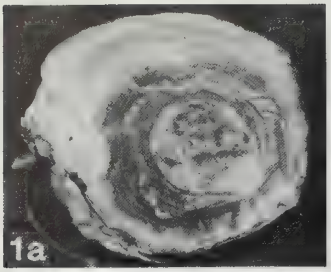
(Evidence of either fluvial or lacustrine aquatic environment is given by pantolestids, chelonians, crocodilians, characoid fish (Gaudant 1979), unionids and quartz-grain tubes of ?Trichoptera).

3. Terrestrial:
   - a. ?insect burrows (for aestivation, hibernation or pupation etc.);
   - b. land snails and slugs;
   - c. well-preserved associated teeth of terrestrial mammals showing little evidence of predepositional transport.

Examples from each of the three groups can be found together in the same hand specimen, so it is unlikely that the disturbed nature of the strata with consequent mixing of layers of different environmental composition can account for this phenomenon. Although a water body of some sort is definitely suggested, there is no evidence that this was very deep. In fact the rarity of pantolestids, crocodilians and chelonians (and small size of the last two, ?juvenile), normally abundant in the vertebrate faunas of the dominantly fluvio-lacustrine (Insole 1972) Headon and Osborne Beds, Bembridge Marls and Hamstead Beds, suggests that it may not have been deep enough to support such a community. Alternatively, their potential food supply might have been excluded by cyanophyte-produced toxins (see Shelubsky 1951).

i. NOTES ON ASPECTS OF THE BIOTA. Cyanophyta: Recent fluvial and lacustrine cryptalgal structures have identical morphology, according to Jones & Wilkinson (1978), but if only infrequently agitated by waves or currents as in a lake, their banding is thinner on the side of the oncolith in contact with the substrate. Some of the Creechbarrow oncoliths show this form (Hudleston 1903: pl. 11, figs 2–4). In temperate climates (Lake Michigan) Jones & Wilkinson noted a seasonal growth pattern, with most activity in the summer, causing annual layers. In subtropical climates (Florida Everglades) a more complex pattern is produced by short wet and dry periods superimposed on overall wet summer and dry winter seasonality (Monty & Hardie 1976). The Creechbarrow cryptalgal structures are laminated irregularly and in places show scattered branched and unbranched radial filaments (Pl. 35, fig. 1c). In gross structure they are nearly all oncoliths ranging from a few millimetres to a few centimetres in diameter. Most commonly they encrust the fresh-water snail shells (Preece 1980*a*: pl. 4, figs g, h), but they also occur without an obvious nucleus or as apparently hollow cylinders, now filled with limestone matrix and perhaps once formed round twigs, stems or roots, growing or loose (Pl. 35, figs 1–2). One in particular is a straight symmetrical cylinder with faint longitudinal striations on the inside wall and with the encrustation recrystallized to radiating fibrous calcite crystals which give the outer surface a knobbly appearance (Pl. 35, fig. 2). Only one fragment of cushion-shaped stromatolite has been found. When complete it would have been no more than about 10 cm across and it appears to have had more than one gastropod nucleus. Daley (1974) described well-preserved material of two new genera of encrusting cyanophytes from the brackish Bembridge Marls of the Isle of Wight.

?Trichoptera larval cases (Pl. 35, fig. 3): Both specimens are fragments of curved wall composed of a mosaic of subangular quartz grains 0·2–0·8 mm in diameter. They had formed nuclei for algal growth and were only discovered by random breakage in processing (or subaerial weathering) of oncoliths. The curvature suggests an original diameter of *c.* 4 mm. The larger of the two fragments has an incomplete minimum length of 6 mm. Polychaetes (e.g. *Sabellaria*) are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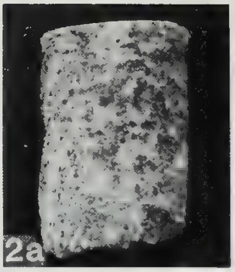
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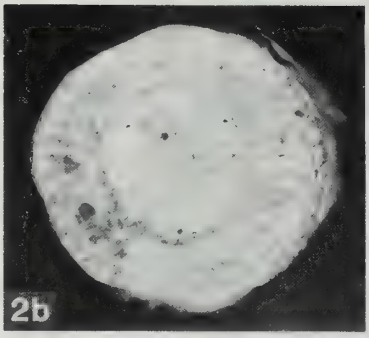
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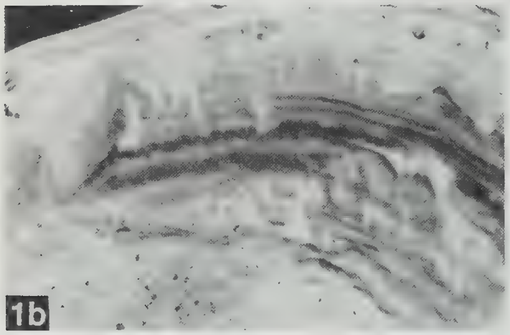
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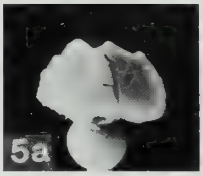
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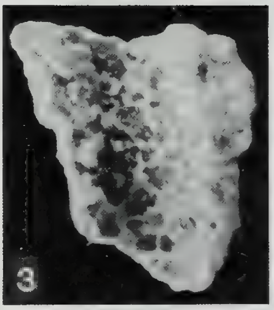
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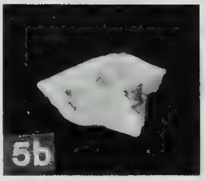
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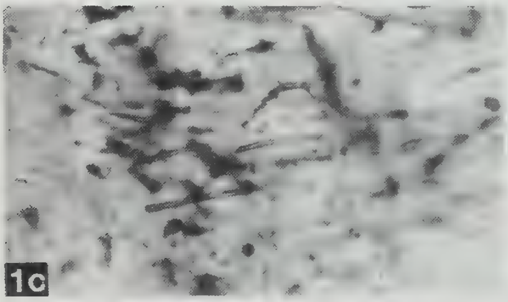
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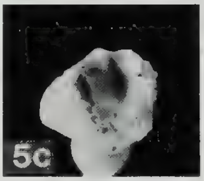
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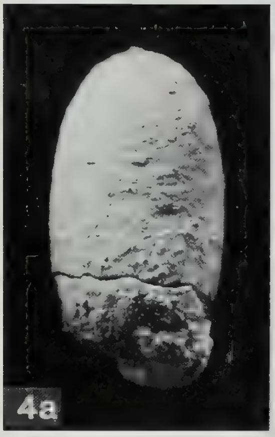
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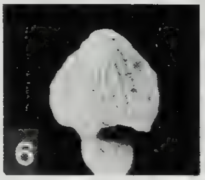
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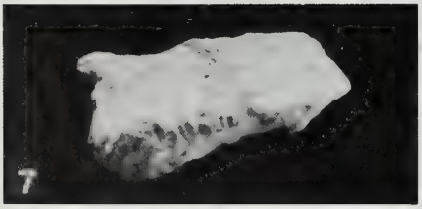
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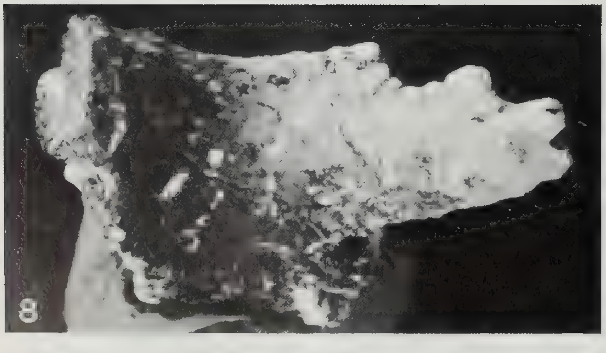
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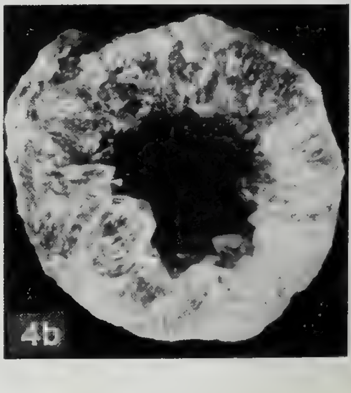
4b

known to construct similar tubes but have generally not become established in fresh-water environments (Chamberlain 1975). Vialov & Sukatsheva (1976) have reviewed the geological record of caddisfly larval cases. Organic-walled types are known from the Palaeogene of western Europe in the Middle Eocene of Geiseltal (D.D.R.) (Haupt 1956) and the Palaeocene of the Isle of Mull (Zeuner 1941). Caddis larvae that construct sandy tubes are more typical of lotic (e.g. fluvial) environments, although some occur in more lentic areas (e.g. lakes) (Chamberlain 1975). Whereas there is insufficient evidence to assign these fragments to Trichoptera with certainty, there is nothing about the specimens to prevent such an attribution (personal communication, P. Barnard 1982).

?Chironomidae larval tubes (Pl. 35, fig. 1b): Randomly orientated, calcite-lined, sparite-infilled tubes occur within oncoliths. Similar structures in marine Triassic stromatolites have been described as the problematicum genus *Microtubus* Flügel 1964, a probable polychaete (see also Wright & Mayall 1981). Modern associations of chironomid larvae and cyanophytes led Anadón & Zamarreño (1981) to recognize as chironomids similar tubes in non-marine Palaeogene oncoliths from Spain. In a modern fresh-water environment with cyanophytes, chironomids are the most likely producers of such tubes, but there is limited morphological support for this attribution (personal communication, P. Cranston 1982).

?Insect burrows (Pl. 35, fig. 4): These also occur in the Bembridge Limestone, where they were originally described as eggs of either turtles or the land snail '*Bulimus*' *ellipticus* (Edwards 1852). White (1921*a*: 117) called them ovoid concretions. Keeping (1910) was the first to record them from Creechbarrow. Preece (1980*a*: 177) called them oviform bodies and compared their spiral grooves to 'the mandibular pattern present in wasp nests'. Their calcite composition appears to constitute a geodal filling of a cavity. Ratcliffe & Fagerstrom (1980) noted that cydnid hemipterans make cell-shaped burrows without access shafts and several other insect groups make vertical or oblique burrows with ovoid terminal cells (trace fossil *Amphorichnus* Myannil 1966). None of the Creechbarrow or Bembridge Limestone bodies appear to have had an access shaft and their orientation in the rock is not recorded as they are normally found weathered out. Their presence nevertheless appears to suggest subaerial conditions.

Tubular burrow: A single slightly flexed tubular limestone burrow fill with no surface structure has been found. It is 45 mm long with a diameter of 10–12 mm.

Fresh-water molluscs: Daley (1972*a*: 27), reviewing earlier studies, stated that *Viviparus* and *Melanopsis* (probably a modern analogue of *Coptostylus*) live today in rivers, ponds, lakes and canals, grazing bare, soft bottom muds. He noted that whereas *Melanopsis* appears to prefer areas free from aquatic vegetation, *Viviparus* will live in marshes; and that whereas *Viviparus* is sensitive to salinity increases above 3‰, *Melanopsis* is tolerant of brackish and fresh water. The occurrence of *Viviparus* at Creechbarrow is an important indication of fresh water, although the abundance of *Coptostylus brevis* suggests near optimum conditions for this species. Preece

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Plate 35 Light macrographs of miscellaneous Creechbarrow biota. Figs 1–3, 4b are not sprayed with ammonium chloride.

Fig. 1a–c Transverse section of cyanophyte oncolith (V.61740); a, complete view of polished face, showing concentric laminae and thinning on one side, × 1; b, details of laminae and associated ?Chironomidae tubes, × 4; c, filaments (one branched), × 500.

Fig. 2a, b Regularly cylindrical oncolith recrystallized to radiating acicular crystals but with a few concentric laminae remaining (V.61741); a, side view, × 1·5; b, polished face, × 3.

Fig. 3 Fragment of oncolith coating part of ?Trichoptera larval case, composed of sand grains, (In.64609), viewed from inside, × 6.

Fig. 4a, b ?Insect burrow (GG21472); a, side view, × 2; b, broken end showing geodal calcite infilling, × 4.

Fig. 5a–c Tooth of characoid fish (P61171), × 7; a, buccal view; b, occlusal view; c, lingual view.

Fig. 6 Crocodilian tooth (R10006), × 5·5.

Fig. 7 Bone fragment of indeterminate ?mammal with gnaw marks (M37572), × 6·5.

Fig. 8 Fragment of mammalian scapula with gnaw marks (M37573); medial view with glenoid to left, × 3.

(1980*a*: 178) suggested poorly vegetated or bare lime mud surfaces to account for the abundant assemblage of *Coptostylus*, the absence of Planorbidae and near absence of Lymnaeidae.

Absence of ostracods and charophytes: This may be diagenetic rather than original. Recrystallization in the limestone has destroyed the fine detail on the larger shells and it is likely that small calcareous organisms would have been obliterated completely. See also comments by Preece (1980*a*: 178).

ii. PROBLEM OF DISTINCTION OF STROMATOLITES FROM CALCRETES. This subject has been discussed by Read (1976). Insole (1972) described various limestones in the Osborne Beds and Bembridge Limestone, which he considered to represent calcretes. In the case of the limestone in the Osborne Beds at Headon Hill, a sequence of marls passing up through nodular limestone is superficially similar to that at Creechbarrow. The Creechbarrow sequence differs in the presence of oncoliths rather than nodules. The limestones themselves also differ. The limestone in the Osborne Beds is vertically fissured and brecciated and the cavities have surface rinds, which is consistent with the structure of calcretes (see Hay & Reeder 1978). Goudie (1973: 23) noted that an important component of calcrete is silica (average 12·3%), including both quartz grains and amorphous silica cement. The Creechbarrow Limestone, in its lack of brecciation, fissuring and amorphous silica cement (the latter was not found in insoluble residues – see methods section, p. 194), is more consistent with an algal than a calcrete origin for the oncoliths. It cannot be excluded, however, that above the modern erosion plane at Creechbarrow, higher parts of the succession now missing may have shown evidence of pedogenesis. This can be associated with terminal regressive phases of lacustrine sequences (e.g. Engesser *et al.* 1981, Goudie 1973) and could account for the recrystallization and poor or non-preservation of small calcareous fossils in the Creechbarrow Limestone.

iii. CONCLUSIONS. Preece (1980*a*) discussed the contrasting views of Hudleston (1902*a*), who thought the Creechbarrow Limestone represented deposition in a lake, and Bury (1934), who considered it a swamp, and partially favoured Bury because of the rarity of land shells in modern lake deposits. Bury was comparing the Limestone with the nearby Holocene tufa of Blashenwell. Preece (1980*b*) concluded that the Blashenwell tufa was deposited on marsh-ground with some water flow and boggy pools. In his list of recorded gastropods, nearly all are terrestrial and none are totally aquatic, a situation different from Creechbarrow. Moreover, his suggestion that 'the nodular or pisolitic lithology and even encrustation of gastropod shells is suggestive of flowing water or seepages' is not corroborated by Jones & Wilkinson (1978), who demonstrated that pisolitic growth can take place, admittedly at a slower rate, on the underside of the body in contact with the sediment.

Several of the features of the Creechbarrow Limestone are consistent with environments found in the 'interior marshes' of the Florida Everglades (see Monty & Hardie 1976). Modern environments in this area have several times been invoked as possible analogues to various late Eocene/early Oligocene deposits of southern England (e.g. Machin 1971, Keen 1977, Collinson 1983). Salient points drawn from Monty & Hardie (1976) which fit the data from Creechbarrow are: the total fresh-water nature of the area; rainy summers and dry winters with superimposed smaller scale wet and dry periods favouring growth of cyanophytes but discouraging aquatic higher plants; cyanophytes able to grow in depths from a few cm to a few tens of cm; environment very quiet. The main features which do not fit the data from Creechbarrow are: the more continuous nature of the algal mat; the absence of sandy detrital deposition; and the calcareous nature of the bedrock substrate. At Creechbarrow the calcium carbonate is likely to have been derived from erosion of nearby Chalk, as the unworn flints and derived Bryozoa (p. 420) testify; the more restricted growth of algae and the detrital elements suggests that the environment was only intermittently quiet.

A Palaeogene non-marine to paralic complex in the Ebro Basin, Spain, with one facies similar to that at Creechbarrow, has been described by Anadón & Zamarreño (1981). This was interpreted as a 'palustrine setting in relation to alluvial fans'. The facies consisted of calcareous mudstones and argillaceous or sandy limestones; the algal bodies were mainly small asymmetric oncoliths (up to 3 cm in diameter and 10 cm in length) with chironomid tubes. This was interpreted as representing marshes and shallow lakes, strongly influenced by sheet floods from the alluvial fans.

Thus it is possible to envisage for Creechbarrow a shallow fresh-water lake to marsh environment, moderately favourable to the growth of oncolitic cyanophytes and to the existence of mud-browsing gastropods and unionid bivalves. This would be subject to periodicity: a, flooding, which introduced clastic detritus and land-derived vertebrates as thanatocoenoses; and b, lowering of the water level, which inhibited algal growth and provided emergent marginal areas which were burrowed by insects and colonized by land gastropods and presumably some land plants.

The environment of deposition between Creechbarrow and Hengistbury will remain unknown as modern erosion has penetrated to much lower strata over the whole area. However, the evidence of progradation of coastal sand in the upper part of the cycle 3, and brackish elements in the otherwise typically marine A3 fauna in Christchurch Bay, e.g. *Theodoxus* spp., *Paludestrina* sp., *Melanopsis* cf. *subfusiformis*, *Batillaria* cf. *calcitrapoides* and *Potamides* cf. *variabilis* (see Burton 1933), suggests that there may have been an intervening hyposaline lagoon.

Tectonic hypothesis. Alluvial fans are known to develop from abrupt topographical features, often fault scarps (Reineck & Singh 1980: 298). If the poorly sorted sands, clays and conglomerates beneath the Creechbarrow Limestone are correctly interpreted as alluvial fan deposits (see above), then we might expect some such feature to have existed in Bartonian times, roughly to the west of Creechbarrow.

Faulting is present in east Dorset south of Creechbarrow in the form of the Ballard Down Fault which trends east–west through the Isle of Purbeck. Small (1980: 52, fig. 1) intepreted this as having been active before the deposition of the Creechbarrow Limestone, on the grounds that 'Creechbarrow type' flints occur in solution hollows in the Chalk south of Creechbarrow. He thus ignored Arkell's (1947: 241) *caveat* that the flints could have been redeposited long after initial deposition in the Eocene.

East–west *en echelon* folds affecting the Hampshire Basin Palaeogene deposits have been attributed by Shearman (1968) to NW–SE dextral wrench faulting in the Palaeozoic basement, following pre-existing joint directions, which can be seen at the surface today in Devon and Cornwall. For details of these structures in SW England see Dearman (1964) and Palmer (1975), and references therein. Shearman considered that the movements in the basement were transmitted upwards into the Mesozoic and Cainozoic cover in the form of these folds accompanied by a décollement. He repeated an experiment by Pavoni (1961) in which wet tissue was placed over two boards. When the boards were slid past each other dextrally in a SE direction, *en echelon*, sigmoidal folds trending east–west were produced in the tissue across the line of displacement. No northerly inclined asymmetry, as occurs in the Hampshire Basin, was produced, but Shearman accounted for this by décollement, which did not occur in the experiment.

All these authors accepted a Neogene date for the faulting and folding, i.e. long after deposition of the Creechbarrow Limestone. Important lines of evidence are: 1, the youngest beds preserved in the Palaeogene sequence (Oligocene Hamstead Beds) are affected by the east–west striking folds; 2, the Oligocene deposits of the Bovey Basin are affected by NW–SE dextral wrench faulting; and 3, penecontemporaneous Palaeogene folding and facies lineation in the Hampshire and Paris Basins have a NW–SE trend (see Fig. 69; Murray & Wright 1974: figs 25E–F, 28; Daley & Edwards 1971; Pomerol 1967). This argues against the model of Small (1980) and suggests that a NW–SE trending feature in the area of central Dorset may have propagated the Creechbarrow fans. No superficial faults of this trend have been detected in this area but a feature of similar orientation occurred a little further to the east in late Albian and Cenomanian times. This is known as the Mid-Dorset Swell. It caused a drastic thinning of deposits and hardgrounds in its vicinity and its existence has been attributed to movements in Palaeozoic basement structures (Drummond 1970). Plint (1982) has provided sedimentological evidence in support of Eocene activity along the east–west fault and fold axis of Purbeck and the Isle of Wight. His evidence, however, could equally be used to support a NW–SE fold structure, which would better fit the other evidence. Moreover, his palaeocurrent direction for M. Eocene meandering rivers is to the north-east (Plint 1983: fig. 12).

If NW–SE normal faulting with downthrow to the NE had occurred in the Palaeozoic basement in later Eocene times in central Dorset, slightly SW of the Mid-Dorset Swell, a NE-dipping monocline would have been produced in the Mesozoic and Tertiary cover. The monocline would have been obliterated by the much severer folding and faulting of the Neogene. Such a tectonic model could not only account for the Creechbarrow alluvial fans but also the successive rapid marine transgressions by intermittent activation of the monoclinal structure causing subsidence on the down-dip side. The clastics would thus have been available to fill much of the marine as well as the alluvial part of the basin between each transgression.

The glauconitic nearshore facies is more restricted in the Barton Clay Formation than in the Bracklesham Group. Deeper water clays are reached more rapidly in an offshore direction and facies change takes place over a shorter distance (e.g. interdigitation of J with K over a distance of *c.* 1 km at Barton). Moreover, the braiding of the rivers presumed to have formed the alluvial fans contrasts with the meandering rivers considered responsible for the earlier fluvial western facies coeval with the marine Bracklesham Group (Plint 1983). All this suggests greater topographic relief, a more rapidly prograding shoreline with a steeper palaeoslope, and stronger current action during early stages of the cycles. See Text-fig. 69 for Hampshire Basin Bartonian facies map.

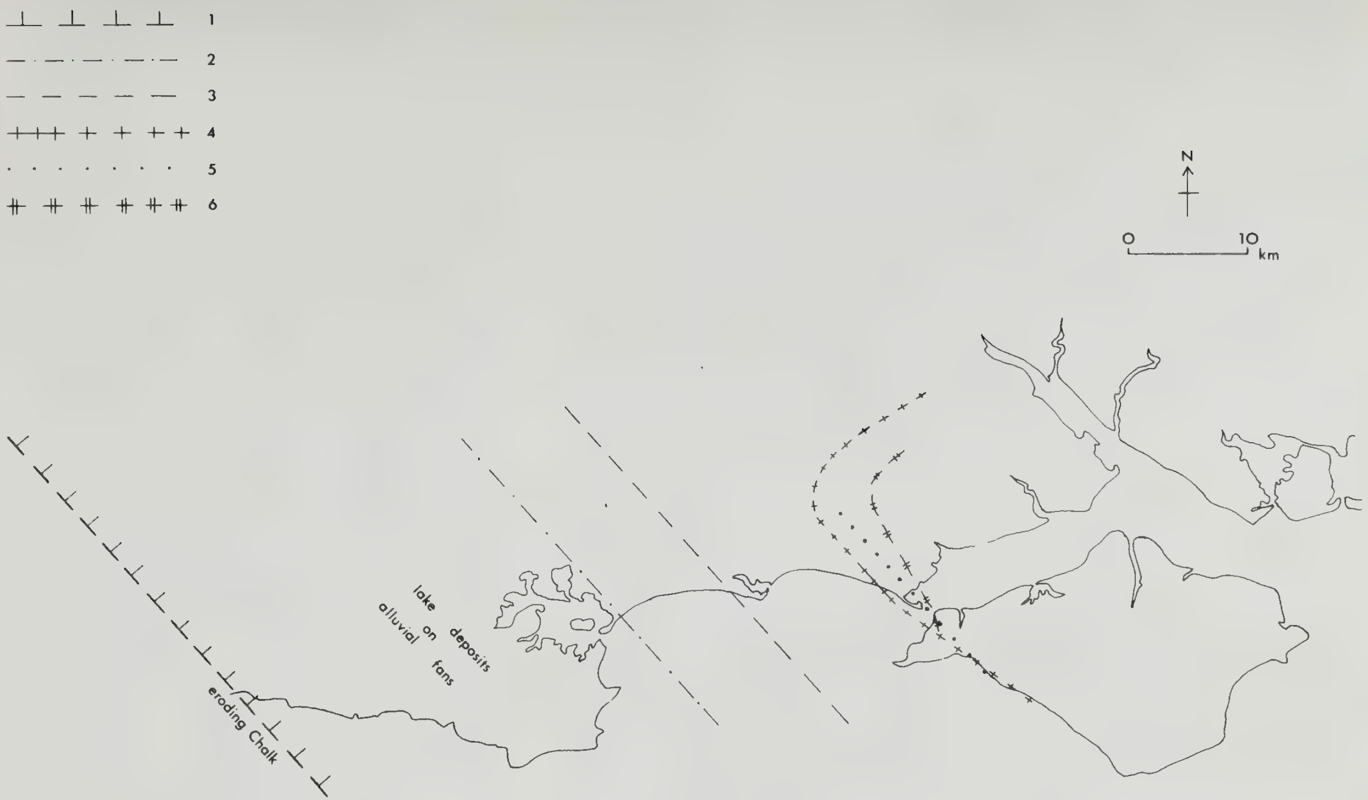
If Shearman's experiment is repeated with the NE plank at a slightly lower level than the other, simulating primary normal faulting, the folding produced by secondary dextral wrench faulting is overturned to the north on the downthrow side. This simulates the asymmetry of the Purbeck monocline without the necessity of a décollement.

Palaeoecology of the Creechbarrow mammal fauna.

Introduction. The restricted total outcrop, poor exposure and disturbed state of the Creechbarrow Limestone Formation make most aspects of taphonomic and palaeoecological analysis difficult or impossible. On the positive side, unlike most other English Palaeogene deposits, no surface collecting could be done and all but three specimens, found during excavation work, were recovered by systematic sieving techniques. Of the matrix collected, about 1600 kg has been completely processed (with the exception of the larger limestone fragments), the remainder being initially searched for only larger mammalian specimens. The proportional abundances of the mammal specimens recorded from this 1600 kg sample can therefore be viewed with some confidence. Immediate areas of bias are likely to be against: 1, those mammals without teeth like the pangolins (Pholidota) and anteaters (Xenarthra), both of which are known from the Lutetian of Messel, W. Germany (Storch 1978, 1981), but unknown at Creechbarrow (see p. 441); and 2, the larger herbivores and carnivores because of the restricted outcrop and poor exposure (see p. 207). Less accountable problems are the impossibility of knowing how accurately the fossil sample reflects the composition of the living assemblage. For a review of these types of problems and bias in assessing modern mammalian populations, see Western (1980).

Preservation. The mammal remains consist predominantly of teeth with relatively few bony skeletal parts being found. The teeth range in appearance from fresh, with mahogany-coloured enamel and slightly darker dentine, to worn and battered with an overall dark brown colour. Some apparently unabraded teeth are almost white; these seem to belong to the first preservational category, but recent weathering has leached them. Manganese is frequently found coating the teeth and is probably also responsible for the dark staining. In preservation bones range from unworn but weathered and white, to worn and of a dark brown colour. Some bones can be worn and light-coloured and have probably undergone leaching like the light-coloured teeth. No preservation is restricted to any particular taxon unless it happens to be very rare or unique.

It is considered that, whereas fluvial transport probably brought most of the specimens into the depositional environment, the more worn and dark-coloured specimens have been carried



Text-figure 69 Map of Hampshire Basin Bartonian facies and palaeogeography. 1 = hypothetical north-east dipping monocline; 2 = postulated position of maximum shoreline; 3 = probable south-west limit of glauconitic beds; 4 = known (continuous) and extrapolated (dashed) south-west and north-west limits of Barton Clay bed J (and lithological equivalents away from Christchurch Bay); 5 = postulated north-eastern limit of regressive sands of cycles 1 to 3; 6 = postulated easterly limits of Becton Sand bed I (and lithological equivalents away from Christchurch Bay). Sources of data: Curry (1942), Hooker (1975), Reid (1898, 1902*a*, *b*), Whitaker (1910, 1917) and White (1921*a*, *b*).

some distance, whilst the fresher specimens probably died much closer to the depositional site. A scatological origin is thought to be unlikely or at least an unimportant factor for two reasons. Firstly there is a complete gradation between the end members of the two preservational types, suggesting continuously varying distances of origin. Secondly the worn appearance of the tooth crowns coincides in most cases with loss of roots, indicating fluvial transport (see Korth 1979), and differing from the enamel-less but rooted teeth considered by Fisher (1981*a*, *b*) to have been excreted by crocodilians. This accords with the rarity of crocodilians at Creechbarrow. Moreover, the preservation lacks the characteristic corrosion typical of certain avian predators (Mayhew 1977).

Some of the better-preserved teeth have been found to be associated, according to their matching interstitial facets as well as their similar natural wear and preservation (e.g. *Lophiotherium siderolithicum* M36177 and M37705, p. 351; and *Haplobunodon venatorum* M37716 and M37529, p. 405). M^{1-3} of *Dacrytherium elegans* (M37177, p. 410) were found in a row, but slightly separated from one another and without the jaw, in a block of limestone. The main specimen of *Plagiolophus curtisi creechensis* (M36181, p. 364) consists of associated upper and lower jaws on both sides as well as numerous unreconstructable jaw fragments. It seems a remarkable coincidence that one of only two specimens of the same species from the marine Barton Clay should also have both upper and lower jaws associated. Single teeth in jaws have occurred in two cases: *Haplobunodon venatorum* (M37544, p. 408) found in the field; and *Gesneropithex figularis* (M35407, p. 234) found separated in residues, but where the broken root surfaces on tooth and jaw were found to match up. The few other jaws found were all edentulous and this condition may be due largely to recent weathering of the deposit.

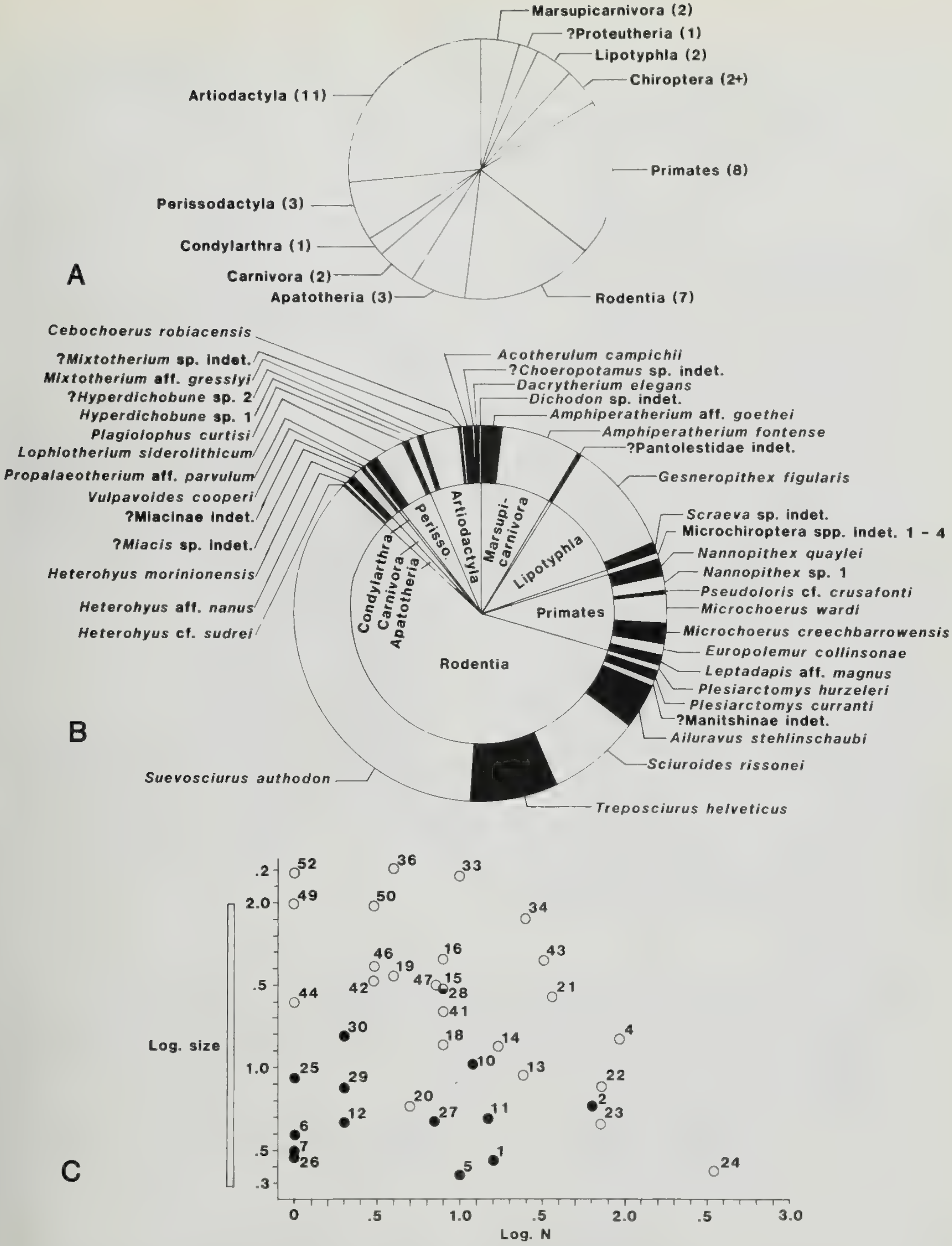
Three isolated teeth have been found in limestone blocks. They belong to *Plesiarctomys curranti* (M35450, p. 285; Pl. 13, fig. 7), *Lophiotherium siderolithicum* (M37446, p. 351) and *Acotherulum campichii* (M36802, p. 400). All are dark-coloured, battered and rootless.

Some of the bones (both fresh and worn) show evidence of rodent gnawing (Pl. 35, figs 7–8). In some cases the marks are transverse to the long axis and occur as parallel grooves; in another they occur round a bite notch (see Bonnichsen 1979 and Morlan 1980 for modern examples). Those on a scapula fragment (Pl. 35, fig. 8) are of appropriate size for the incisors attributed herein tentatively to *Suevosciurus authodon*. Those figured in Pl. 35, fig. 7, however, appear to have been made by much smaller teeth. If these were of a rodent, it must have been smaller than any recorded from teeth at this locality.

Faunal Composition. Text-fig. 70A–B shows relative abundances based on the ordinal composition of species and individuals respectively. They show that whereas the artiodactyls display the greatest diversity of species, the rodents make up over 50% of the individuals (more than a third belonging to *Suevosciurus authodon*). The apatotheres, whilst showing some diversity, are few in number of individuals. They were also found to form only *c*. 1% of North American Eocene faunas (West 1973). Creechbarrow seems notable for having representatives of groups normally rare in European Eocene deposits, i.e. one paroxyclaenid, three apatotheres, two *Plesiarctomys* and a third undet. manitshine, and *Ailuravus*. This may be more a feature of the bias against smaller mammals in old collections from the main Lutetian and Bartonian localities and the increasing rarity of these groups from late Bartonian times onwards. The latter feature is particularly relevant to the locality of Robiac.

Text-fig. 70C shows log. of maximum numbers of specimens per species for the 1600 kg sample plotted against log. of size based on M^1 area (or the best approximation to it when this tooth was not available). Creighton (1980) showed that area (length × width) of M_1 correlated accurately with body size in modern mammals (except edentates). M^1 is preferred here because length and width are usually approximately equal and can thus be more easily extrapolated, when only lower teeth are available. In certain mammals, e.g. rodents, M^1 and M^2 are essentially the same size and their mixing for statistical purposes still produces a low coefficient of variation.

In Text-fig. 70C, species considered on their dental morphology to be at least mainly frugivorous or herbivorous plot in broad linear fashion, becoming less abundant with increasing



Text-figure 70 Diagrams of relative abundances of Creechbarrow mammals.

A. Circular diagram showing proportional representation of species numbers per order.

B. Circular diagram showing proportional representation of specimen numbers per species, grouped by order.

C. Scatter diagram of log. size (based on M^1 area, or its extrapolation by squaring M_1 length) against log. numbers of individuals (based on maximum numbers of teeth). Bar on left gives range of size of modern arboreal herbivores from Eisenberg (1978) extrapolated to tooth size using Creighton (1980). Outline circles are probable herbivores; solid circles are probable insectivores/carnivores; numbers against symbols refer to taxa listed in Table 1, pp. 212–215.

size. Those species considered on dental morphology to be mainly insectivorous or carnivorous are rarer in occurrence than the equivalent-sized herbivores. There is some overlap, however, the herbivorous ?*Mixtotherium* sp. indet. and cf. Manitshinae indet. being exceptionally rare and the carnivore ?*Miacis* sp. indet. and possible carnivore *Amphiperatherium fontense* being relatively common.

The correlation of increasing rarity with increasing size in the herbivores may reflect generally more scattered populations of animals with greater biomass, or it might reflect their lower birth and death rates (see Western 1980). This ignores possible gregarious versus non-gregarious habits, simple rarity or abundance of particular species, range of habitats sampled and many other unknowns. However, as a general rule, insectivore-carnivores tend to be rarer than frugivore-herbivores for a given size (Wolff 1975). Moreover, the consistency in the range of good to poor preservation for all the taxa suggests that even if areas at different distances from the depositional site have been sampled, the same fauna occurred throughout.

The correlation of herbivore size and abundance plus the presence of the rhinoceros-sized herbivore *Lophiodon* cf. *lautricense* in nearly contemporaneous marine deposits at Hengistbury suggest that larger herbivores and probably carnivores may once have lived in association with the Creechbarrow fauna as known at present, but are missing on account of inadequate sampling. The range of larger perissodactyls and artiodactyls as well as the larger creodonts and carnivores present in such Bartonian localities as Eclépens-Gare and Robiac also supports this. If the linear plot of Text-fig. 70C is continued to the log. M^1 area of *L. lautricense* (3·34 calculated from Sudre's 1971 measurements), it can be calculated that somewhere in the region of 30 tonnes of Creechbarrow Limestone would have to be processed in order to find even a single individual of this species (if present).

Korth (1979) determined a sequence of fluvial deposition of different mammalian skeletal elements from settling and flume experiments. Particular elements grouped into five categories. Generally poor preservation of bone at Creechbarrow prevents a direct comparison with his categories, because of the likelihood of bias against those which were small and fragile and those that were large and little transported (i.e. less mineralized and liable to shattering to an unrecognizeable condition). Nevertheless a large range of different elements of different sizes and different preservation states are present. Complete or fragmentary rib (1), radii (2), ulna (1), calcanea (2), femur (1), mandibles (10), tibia (1), metapodials (6), podials other than calcaneum and astragalus (3), phalanges (5) and sesamoids (3), as well as the many teeth, were recovered from the 1600 kg sample. In addition, fragments of a vertebra, pelvis, scapula and astragali have been recovered from other samples.

Notes on diet, habits and habitat. Table 39 lists the Creechbarrow mammal taxa with, for each, a suggested nearest living relative (column 1), modern taxon with similar teeth (if available) (column 2) and where possible a relevant nearest relative from the early Lutetian of Messel, B.R.D., where articulated skeletons often with soft parts and gut contents are known (column 3). In many cases the first column will be irrelevant, particularly in the case of totally extinct family or higher taxa. If, however, this is the same as, or closely related to, the taxon in the second column, the significance of the latter is reinforced. Column 3 is important either as a back-up or in the absence of a column 2 taxon. Comments on the possible ecology of the Creechbarrow mammals are given below, incorporating the Table 39 data.

DIDELPHIDAE. Crochet (1980: 230) noted that an arboreal habit predominates in modern didelphids, but some are ground dwellers and one a specialized aquatic. He also noted that their diet is very varied from insectivorous, carnivorous to granivorous and frugivorous, and that whereas there are different dietary specializations between different species, the overlap is great. He suggested (1980: 231–232) that the structure of the humerus in the extinct *Peratherium* might indicate less arboreality than modern forms; but preferred the idea that it reflected some unknown specialization of the European Tertiary forms. He also suggested that the teeth of the genus *Amphiperatherium* showed a tendency towards carnivory.

Table 39 Nearest living relatives and modern dental analogues of the Creechbarrow mammals. The third column gives the relevant nearest relative in the Lutetian fauna at Messel, B.R.D.

Creechbarrow taxon	Nearest living relative group	Modern analogue with some similar teeth	Nearest Messel relative
Amphiperatherium aff. *goethei*	Didelphini	*Marmosa*	
A. fontense	Didelphini	*Marmosa*	
?Pantolestidae indet.	?		*Buxolestes piscator*
Gesneropithex figularis	Erinaceidae?	*Neotetracus*	*Pholidocercus hassiacus*
Scraeva sp. indet.	Erinaceidae?	*Ptilocercus*	
Microchiroptera indet. 1–4	Microchiroptera	most insectivorous microchiropteran families	Microchiroptera
Nannopithex quaylei	*Tarsius*	*Microcebus*	
N. sp. 1	*Tarsius*	*Microcebus*	
Pseudoloris cf. *crusafonti*	*Tarsius*	*Tarsius*	
Microchoerus wardi	*Tarsius*		
M. creechbarrowensis	*Tarsius*		
Europolemur collinsonae	Lemuroidea	*Alouatta*	Adapidae indet.
Leptadapis aff. *magnus*	Lemuroidea	*Hapalemur*	
Adapinae indet.	Lemuroidea		
Plesiarctomys curranti	Rodentia	*Ratufa*	
P. hurzeleri	Rodentia	*Ratufa*	
?Manitshinae indet.	Rodentia		
Ailuravus stehlinschaubi	Rodentia	*Petaurista, Trogopterus*	*A. macrurus*
Sciuroides rissonei	Rodentia	*Iomys*	*Masillamys krugi*
Treposciurus helveticus preecei	Rodentia	*Iomys*	*Masillamys krugi*
Suevosciurus authodon	Rodentia	*Iomys*	*Masillamys krugi*
Heterohyus cf. *sudrei*	Ferungulata?	*Dactylopsila, Daubentonia*	
H. aff. *nanus*	Ferungulata?	*Dactylopsila, Daubentonia*	
H. morinionensis	Ferungulata?	*Dactylopsila, Daubentonia*	
?*Miacis* sp. indet.	Carnivora		*Paroodectes feisti*
?Miacinae indet.	Carnivora		*Paroodectes feisti*
Vulpavoides cooperi	Ungulata	see p. 446	*Kopidodon macrognathus*
Propalaeotherium aff. *parvulum*	*Equus*		*P. messelense*
Lophiotherium siderolithicum	*Equus*		*P. messelense*
Plagiolophus curtisi creechensis	*Equus*	*Dendrohyrax*	*P. hassiacum*
Hyperdichobune sp. 1	Artiodactyla		*Messelobunodon schaeferi*
?*H.* sp. 2	Artiodactyla		
Mixtotherium aff. *gresslyi*	Artiodactyla	*Indri, Propithecus*	
?*M.* sp. indet.	Artiodactyla		
Cebochoerus robiacensis	Artiodactyla	*Cercocebus albigena* *Cercopithecus pogonias*	
Acotherulum campichii	Artiodactyla	*Cercopithecus pogonias*	
Haplobunodon venatorum	Hippopotamidae?		*Masillabune martini*
?*Choeropotamus* sp. indet.	Hippopotamidae?		
Dacrytherium elegans	Artiodactyla	*Indri, Propithecus*	
Dichodon cf. *cervinus*	Camelidae?	see p. 447	
D. sp. indet.	Camelidae?	see p. 447	

PANTOLESTIDAE? A semiaquatic mode of life for this family was originally suggested by Matthew (1909) when describing the type genus. This was confirmed by a skeleton of *Buxolestes* from Messel, which has a tail with swimming adaptations and gut contents including fish (Koenigswald 1980*a*). The Creechbarrow specimens are only tentatively referred to the family but may also have been semiaquatic.

LIPOTYPHLA. The cheek teeth of *Gesneropithex figularis* are similar in cusp pattern to those of hedgehogs, but differ in the following important ways: metastylar wing is reduced along with the degree of buccal phase shear; protocone and hypocone crests are better developed along with greater degree of lingual phase wear; cristid obliqua is higher for lingual phase wear; and paracristid is reduced along with general buccal phase shear. The only extant erinaceid where there is any sign of reduction of the metastylar wing and paracristid on the molars is the galericine *Neotetracus*, which has fewer insect and more plant items in the diet than the others (Walker 1975).

A proposed combination of insectivory and frugivory for *G. figularis* from modern dental analogy is supported by the record of plant and insect remains as stomach contents of the amphilemurid *Pholidocercus* from Messel (Koenigswald & Storch 1983: 492). Study of several complete skeletons from this locality led Koenigswald & Storch (1983: 492–493) to conclude that *Pholidocercus* was mainly a waterside ground dweller capable of shallow digging in a moist substrate. *Gesneropithex* is tentatively attributed similar habits, although no postcranial elements are yet known.

Scraeva and other nyctitheres are generally considered insectivorous, but it is difficult to find modern analogues with similar cuspate teeth that are not either nyctalodont or myotodont (Menu & Sigé 1971). The mainly insectivorous (Walker 1975) tupaiid *Ptilocercus* has both anterior teeth and cheek teeth with somewhat similar cusp patterns; but incisor denticulations are missing, intermediate conules are missing on the upper molars and the lower molars are broader, less high-cusped and the cristid obliqua is less oblique. *Scraeva* then appears more distinctly specialized for insectivory than *Ptilocercus*.

MICROCHIROPTERA. Nothing more can be said than that the few teeth resemble those of insectivorous modern Microchiroptera and presumably had a similar diet. That there were Eocene insectivorous bats has been shown by Smith *et al.* (1979) for Messel specimens with gut contents.

PRIMATES. The family Tarsiidae, being monotypic and relict today, cannot necessarily be expected to provide information on all the diverse members of the tarsiiform Omomyidae (see Szalay 1976). Of the Creechbarrow microchoerines, only *Pseudoloris* is really similar dentally to *Tarsius* (Teilhard 1921; Szalay 1976). It probably had a similar insectivorous/carnivorous diet. The species of *Nannopithex* have a modern dental analogue in *Microcebus*, which is mainly insectivorous (Walker 1975). *N.* sp. 1 (p. 251), however, unlike *Microcebus* has wrinkled enamel and may show a slight trend towards herbivory. *Microchoerus* was suggested by Szalay & Delson (1979: 265) to be 'primarily folivorous' because of the predominance of sharp cutting edges on its cheek teeth, maintained throughout wear, although they did find it difficult to decide whether the herbivorous emphasis was on fruit or leaves. The late advanced species *M. edwardsi* exhibits much cusp duplication and accessory crests which would fit an adaptation to folivory (cf. folivorous rodents discussed below). Except for the presence of a molar mesostyle, however, early species, as at Creechbarrow, are very similar to *Necrolemur*, which Szalay & Delson (1979: 262) considered 'highly frugivorous'. Postcranial evidence of incipient typical modern tarsier locomotory specializations is scanty but widespread in the Omomyidae, including the Microchoerinae (Szalay & Delson 1979; Schmid 1979). The five Creechbarrow microchoerines are therefore considered arboreal clinger-leapers with the variety of dietary specializations outlined above.

Szalay & Delson (1979: 125) suggested a frugivorous-insectivorous diet for *Europolemur* (then monotypic). *E. collinsonae*, however, shows specializations paralleling those of *Caenopithecus* in buccal flexing of the molar centrocrista and premolar simplification. Szalay & Delson (1979:

143) suggested *Caenopithecus* was a folivore, comparing it with modern indriids. *E. collinsonae*, in its slightly less *Caenopithecus*-like specializations, was probably therefore frugivorous-folivorous. *Leptadapis magnus* was considered by Szalay & Delson (1979: 139) and Gingerich & Martin (1981: 254) to be probably folivorous. Its tooth pattern is somewhat like the modern folivore *Hapalemur* but the upper molars are relatively longer and the hypocones larger, whilst the lower molars have lower metaconid–metastylid and higher entoconid cusps (see Seligsohn & Szalay 1978).

Fogden (1974) found that modern *Tarsius bancanus* inhabited mainly secondary forest with minor occurrence in the understory of primary forest, avoiding forest canopy, very dense vegetation and also rather open secondary vegetation with dense herbaceous cover. Whether or not extinct tarsiiforms had broader tolerances is not known. Koenigswald (1979) has demonstrated the presence of a typical lemuriform hind foot complete with groom claw in a Messel adapid. According to the evaluations of Decker & Szalay (1974) and Gingerich & Martin (1981: 255), it seems reasonable to consider both *Europolemur collinsonae* and *Leptadapis* aff. *magnus* as arboreal.

RODENTIA. The dental diversity of the Lutetian–Bartonian rodent radiation is paralleled and exceeded by living members of the Sciuridae. For instance, great similarities are shown by manitshine paramyids to *Ratufa*; ailuravine paramyids to *Petaurista* and *Trogopterus*; pseudosciurids to *Iomys*; and even glirids to *Exilisciurus*.

Wood (1962) considered that the manitshine genera *Manitsha* and *Ischyrotomus* were ground-dwelling and possibly subfossorial, but could not be precise on their individual specializations. Unlike these genera, *Plesiarctomys* is unknown beyond the skull and dentition, so questions of arboreality or ground dwelling are impossible to answer. Its cranial and dental similarities to other manitshines make the latter more likely. *P. curranti* has broadly basined cheek teeth with some enamel wrinkling and nearly transverse buccal and lingual phase mastication. It is thus very similar to *Ratufa* which is mainly a frugivore. *P. hurzeleri* has larger blunt-crested cheek teeth, but both species may have been frugivorous.

Arboreal adaptations have been suggested for Messel *Ailuravus macrurus*, including prehensility of the very long tail (40 vertebrae), by Weitzel (1949). Wood (1976*a*: 146) suggested a frugivorous diet for the genus. *A. stehlinschaubi*, however, has cheek teeth with many more accessory crests and wrinkles than has *A. macrurus*, and in these structures it is similar to modern *Petaurista* and *Trogopterus*. *Petaurista* was considered to have an arboreal rating of 4·5 (out of 5) and a herbivory rating of 3·5 (out of 5) by Eisenberg (1978) and was stated to have a diet of leaves, fruit and seeds by Muul & Lim (1978). *Trogopterus* is recorded as feeding on oak leaves (Walker 1975). *Trogopterus* has slightly higher-crowned and more elaborately selenodont and crested teeth, but is otherwise very similar in pattern to *A. stehlinschaubi*, having upper molar hypocones unlike *Petaurista*. Both modern genera, however, have less transverse motion in both buccal and lingual wear phases, although within the *Sciurus* type (see Butler 1980). It is concluded therefore that *A. stehlinschaubi* was arboreal and essentially a folivore.

Iomys shares with the Creechbarrow pseudosciurids squared upper molars with large hypocone joined by metalophule to the metacone, and lower molars with hypolophulid. Of the three pseudosciurids in the fauna, *Suevosciurus* is closest in molar morphology to *Iomys*, but even so is less lophodont than this genus, and wear is less oblique. *Iomys* has a diet of fruit and seeds (Muul & Lim 1978) so it is probable that *Sciuroides rissonei*, *Treposciurus helveticus preecei* and *Suevosciurus authodon* were also frugivorous/granivorous. *Suevosciurus* is known from an almost complete articulated skeleton (*S. ehingensis*, M. Oligocene of Armissan; Lavocat 1955, as *Pseudosciurus suevicus*). Its fore and hind limb proportions and unfused tibia and fibula suggested to Lavocat a primitive scrambler, capable of living both on the ground and to a certain extent in trees, but with no specific arboreal adaptations. This was probably also the case with *Sciuroides* and *Treposciurus* and appears to have been the primitive rodent condition (Lavocat 1955, Wood 1962).

The later (Oligocene) rather restricted distribution of *Suevosciurus* (mainly in southern Germany) suggests some specialization, but the ability of two lineages of this genus to cross the

'Grande Coupure' virtually unchanged suggests some versatility of habits or the occupation of a niche not exploited by the new immigrants. The drastic reduction of *Sciuroides* at the same time as the spread of theridomyids in the early Ludian does not support the theory that both shared similar ecological adaptations (see Schmidt-Kittler 1971*a*: 125–127). The slightly different emphasis of longitudinal (in *Sciuroides*) versus transverse (in *Suevosciurus*) crests is likely to reflect only minor dietary differences.

APATOTHERIA. Stehlin (1916) compared the genus *Heterohyus* with the modern lemuroid *Daubentonia* mainly in search of relationship, but in this he has subsequently been shown to be incorrect. West (1973: 23–24) compared *Apatemys* teeth functionally with those of the phalangerid *Dactylopsila* and concluded that like the latter it too may have been arboreal and used its enlarged incisors for tearing bark open to hunt for insects. Cartmill (1974) compared skull structure in relation to food-gathering function in both *Daubentonia* and *Dactylopsila* and found similar specializations, including clinorhynchy, in both. Scott & Jepsen's (1936: pl. 5) side view of the skull of the Oligocene apatemyid *Sinclairella* suggests a certain degree of clinorhynchy but less than occurs in *Dactylopsila*. Skulls of *Heterohyus* are virtually unknown, but the incisors are robust and higher-crowned than in *Sinclairella* or *Dactylopsila*, although without the persistent pulps of *Daubentonia*. An arboreal mode of life hunting wood-boring insects is likewise envisaged for *Heterohyus*.

PAROXYCLAENIDAE. Some similarities to the reduced bunodont to semi-bunodont cheek teeth of various viverrids (e.g. *Arctogalidea*) and procyonids (e.g. *Bassaricyon*, *Nasua*) are shown by the paroxyclaenid *Paroxyclaenus*. These viverrids and procyonids are mainly frugivorous and partly carnivorous (Walker 1975). Other paroxyclaenid genera (e.g. *Vulpavoides*, *Kopidodon*) have analogues in more insectivorous viverrids like *Bdeogale*, *Crossarchus* and *Eupleres*. Molar size reduction is accompanied by occasional increase in number in *Kopidodon* and also in the modern canid *Otocyon* (see Tobien 1969, Van Valen 1964). An approach to the semi-zalambdodonty of *Vulpavoides* is found in *Eupleres*, although here the teeth are excessively reduced in size and robusticity. No exact modern analogue has been found for the curious high-cusped M^1 of *Vulpavoides cooperi*. *Otocyon* eats insects, especially termites, but is also partly frugivorous and carnivorous; *Eupleres* catches adult and larval insects by digging and also eats small tetrapods (Walker 1975). It is possible that *Vulpavoides* combined insectivory, carnivory and frugivory in its diet in a similar way.

PERISSODACTYLA. The nearest modern relative is obviously no guide to diet in the three Creechbarrow palaeothere genera. However, *Propalaeotherium messelense*, a very close relative of *P. parvulum*, is recorded from Messel with preserved gut contents consisting in one case of leaves of several dicotyledon families (Sturm 1978), and in another of *Vitis* (grape) seeds (Koenigswald & Schaarschmidt 1983). Of the leaves, species of the Lauraceae and Apocynaceae predominate, with Annonaceae or Symplocaceae, Myrtaceae, Juglandaceae and Moraceae as more minor constituents; of these, only the Annonaceae, Symplocaceae and ?Moraceae occur in the poorly-known flora of Bed A3 at Barton Cliff (penecontemporaneous with Creechbarrow). The closely related *Lophiotherium siderolithicum* shows trends in premolar molarization, perhaps towards a coarser diet, but may still have been folivorous-frugivorous.

Plagiolophus curtisi is the largest species in the fauna so far known and has the highest-crowned teeth. These show, however, only incipient trends in hypsodonty and their pattern has been described as selenolophodont. A herbivorous diet, coarser than for either of the other palaeotheres, is suggested. The occurrence of upper and lower jaws preserved together at two localities suggests perhaps powerful jaw muscles. This together with the massive parallel-orientated procumbent canines and robust cheek teeth, unlike other species of the genus, suggests that it may have had rooting habits. This species exceeds the size range for arboreal folivores (see Text-fig. 70C and Eisenberg 1978), and for this and family-wide osteological reasons all three palaeotheres were likely to have been ground dwellers.

The probability of larger herbivorous perissodactyls like *Palaeotherium* and *Lophiodon lautricense* (from penecontemporaneous records from Hengistbury and Barton – see p. 214) having occurred at Creechbarrow is high. The latter's molar specializations resemble those of modern tapirs, which feed on leaves of aquatic and low-growing terrestrial plants, favouring the most abundant taxa (Walker 1975). Fischer (1964: 69–70) compared their mode of chewing with that of both tapirs and pigs. He then, however, stressed the differences from tapirs: e.g. absence of evidence for a proboscis, presence of conical incisors and larger canines in *Lophiodon*. He compared the postcranial skeleton with that of the extinct Pleistocene species of the rhinoceroses *Dicerorhinus* and *Coelodonta*.

ARTIODACTYLA. Estimating way of life of this group from either nearest living relative or modern dental analogue is difficult. There are two relevant Messel skeletons, *Messelobunodon* and *Masillabune*, with gut contents. Those of the dichobunid *Messelobunodon schaeferi* were found to be undetermined fungi along with decayed leaves and it was concluded that it acquired the former by rooting on the forest floor (Richter 1981). *Hyperdichobune* sp. 1 (p. 376), as it is a dichobunid, may have had similar habits, but the molar mesostyle and larger metaconule and incipient P^4 molarization might point to frugivorous or folivorous tendencies.

The gut contents of the haplobunodontid *Masillabune* were found to be leaves (Tobien 1980). The probability that *Haplobunodon venatorum* was also highly folivorous is supported by its convergent dental similarities to *Propalaeotherium* aff. *parvulum*.

Mixtotherium and *Dacrytherium* belong in different families but are dentally rather similar, being low-crowned and strongly selenodont with strong molar and, in the case of *Mixtotherium*, P^4 mesostyles. The closest modern analogues seem to be the indriid primates *Propithecus* and *Indri*. Particular similarities are the configuration of the upper premolars and molars with prominent recurved parastyles, especially like *Mixtotherium*. The main difference is the weakness of the selenodonty in the lower molars and in the lingual cusps of the upper molars. Modern indriids are predominantly arboreal folivores (Kay & Hylander 1978) but the postcranial skeleton of *Mixtotherium* is unknown. That of anoplotheres is, however, typically artiodactyl and it is likely that both genera were ground-dwelling folivores.

Dichodon had higher-crowned selenodont teeth than *Dacrytherium* and was larger, but like *Mixtotherium* P4 was molariform. Its blade-like anterior dentition without diastema was like *Dacrytherium* but appears to have no modern analogue. Modern tragulids and small cervids have higher-crowned molars and different food-gathering apparatus, with incisiform canines and a marked diastema. Modern tragulids are both frugivorous and folivorous but have simpler, less selenodont molars than *Dichodon*. Molars of modern small deer (browsers) are more comparable in their degree of selenodonty and development of upper buccal and lower lingual stylar cusps. It is considered likely that *Dichodon* was primarily folivorous.

Similarities of the teeth of cebochoerids (*Cebochoerus* and *Acotherulum*) to cercopithecid primates misled Filhol (1877*b*) to suggest a relationship between these and suoid artiodactyls (cebochoerids were originally classified as pigs). Similarities in brachyodont bunodont dental pattern of the Creechbarrow cebochoerids to the dominantly frugivorous cercopithecid taxa are striking and suggest a similar diet for them. Once again, the postcranial skeleton is unknown but it is likely that they were ground-living like most other artiodactyls.

Conclusions

This probable community, which is rich in primates, arboreal species generally and species with frugivorous and folivorous diets, is typical of a forest environment, amongst available modern habitat types (see Davis 1962, Nesbit Evans *et al.* 1981). Non-mammal support for this environment is the high proportion of shade-demanding land gastropods (Preece 1980*a*). The number of mammal species (40 excluding bats) is close to that of a modern temperate forest (Davis 1962). However, in view of the likely incompleteness of the Creechbarrow record (see p. 438; and Wolff 1975), the postulated original number (nearly double that recorded) is closer to that of a modern tropical forest (Davis 1962). Buchardt (1978), Châteauneuf (1980), Collinson *et al.* (1981), Daley (1972*b*), Murray & Wright (1974) and Wolfe (1978, 1980) have nevertheless all pointed to a cooler than tropical climate in northern latitudes in the Eocene. The warmest temperatures are thought to occur in the earliest Lutetian or latest

Ypresian, decreasing to a Palaeogene minimum by the end of the Priabonian (≏ late Ludian–early Stampian). The temperatures postulated on isotopic evidence by Buchardt (1978) for the age under discussion fall within the modern forest climate called paratropical by Wolfe (1979). A number of the nearest living relatives and nearest dental analogues of the Creechbarrow mammal assemblage are confined to tropical forest. This probably reflects the results of reliction and retreat from increasing seasonality (Daley 1972*b*) rather than an original geographical and climatic restriction. It is concluded that the Creechbarrow mammal fauna probably inhabited a forest, existing under a paratropical climatic regime. The diversity of tarsioids and of ground-dwelling frugivores and folivores suggests an abundance of low-growing shrubs but without dense herbaceous undergrowth.

No flora is known from the Creechbarrow Limestone, presumably for preservational reasons, but its probable time equivalent the Barton Clay bed A3 at Barton Cliff has yielded some fruits and seeds (Chandler 1960). In terms of nearest living relatives this small flora is thought to include two coniferous trees, three aquatic or subaquatic herbs, three marginal aquatic herbs/shrubs, six shrubs/small trees, two probable lianes and several unknowns (see Chandler 1960, 1964). Unfortunately this is a low-diversity assemblage dominated by those plant organs most likely to survive transport into a marine depositional environment. It is probably not a true representation of the vegetation of the area (Chandler 1964; M. E. Collinson, personal communication 1982).

The spatial relationships of the presumed forest to the shallow lake depositional environment of the Creechbarrow Limestone is unknown. In view of the unsorted appearance of the mammal assemblage it is unlikely to have been far away.

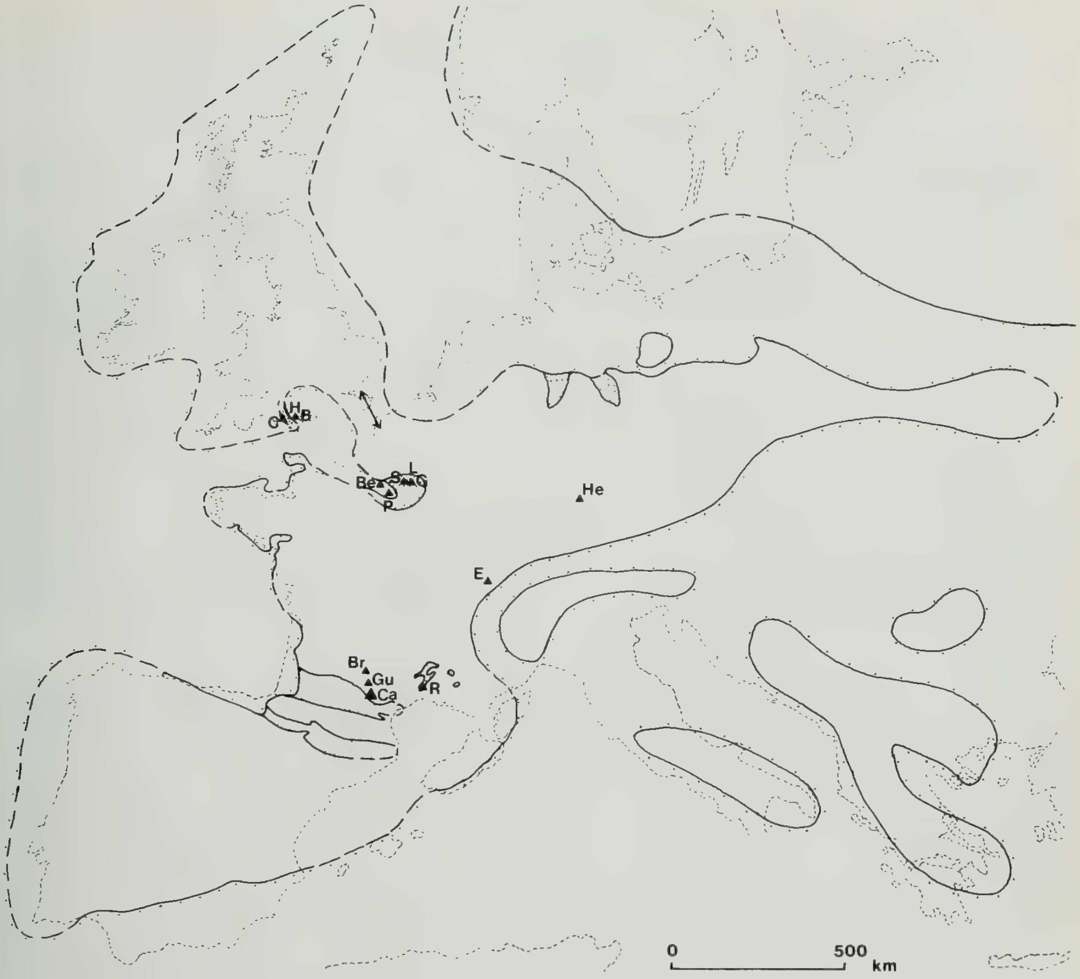
Palaeogeography

Faunal Provinces. Schmidt-Kittler & Vianey-Liaud (1975) and Schmidt-Kittler (1977*b*) divided the main European island area in the late Ludian into several faunal provinces based on rodents: 1, southern England plus Belgium and Germany west of the Rhine Graben; 2, southern Germany east of the Rhine Graben; 3, the Franco-Swiss area; and 4, Spain. At this time the inundated Rhine Graben (and possibly a non-marine area linking the latter to the Paris Basin, see Krutsch & Lotsch 1958) were important physical barriers. The former authors, however, considered that the main reasons for separation were ecological, a forested area existing in southern Germany east of the Rhine Graben, favouring such pseudosciurids as *Pseudosciurus* and *Suevosciurus*.

Franzen (1968: 158–159) distinguished northern and southern faunal provinces in the Ludian based on the genus *Palaeotherium*. His northern province equates with 1 and 2 of Schmidt-Kittler & Vianey-Liaud (1975) and his southern province with their 3 and 4. He noted a tendency for species with short, broad feet to occupy the north and for species with longer and more slender feet to occupy the south. He suggested that the north might have been a damper, more wooded region and the south drier and more open.

Sudre (1978*b*: 192–196) found some evidence from artiodactyls and primates to support Schmidt-Kittler & Vianey-Liaud's (1975) rodent provinces. He also noted endemic forms in the southern English Ludian (see also Sudre 1974), Spain and southern Germany.

Faunal provinces are less easy to envisage in the Bartonian because of the small number of localities, but there seems to be a tendency for endemics such as *Leptolophus*, *Plagiolophus cartailhaci*, *P.* aff. *annectens*, *Elfomys*, *Necrolemur*, *Peratherium*, *Saturninia*, *Adapis*, *Gliravus*, *Paradelomys*, *Pseudoltinomys*, *Anchilophus*, *Xiphodon*, and *Haplomeryx* to occur in the south. There is also a tendency for *Haplobunodon*, *Plagiolophus curtisi*, *Treposciurus*, *Suevosciurus*, *Nannopithex*, *Microchoerus* and *Scraeva* to occur in the north. An important zone of overlap occurs in the Mormont area of Switzerland. At the same time a number of taxa are widespread, e.g. *Lophiodon lautricense*, *Lophiotherium siderolithicum*, *Ailuravus stehlinschaubi* and *Plesiarctomys hurzeleri*. It seems that at least during some of the time there were no geographical barriers to dispersal in the later Bartonian. Evidence from southern Germany is restricted to one species (*L. lautricense*) from one locality (Heidenheim). Sediments of this age are sparse and



Text-figure 71 The palaeogeography of Europe in the Bartonian with *Lophiodon lautricense–Lophiotherium siderolithicum* Zone mammal localities. Fine dashed lines show outlines of modern land masses. Heavy lines show Bartonian coastlines, with dots on the seaward sides. Stipple indicates principal areas of non-marine sedimentation. Two-way arrow indicates position of postulated Weald–Artois land bridge. Abbreviations of localities: B = Barton; Be = Berville; Br = Le Bretou; C = Creechbarrow; Ca = Le Castrais localities; E = Eclépens-Gare and Eclépens A; G = Grisolles; Gu = La Guittardie; H = Hengistbury; He = Heidenheim; L = Latilly; P = Paris; R = Robiac; S = Sergy. Solid triangles indicate positions of localities. Sources of palaeogeographic data: Azzaroli (1981), Boccaletti & Manetti (1978), Krutsch & Lotsch (1958), Lemoine (1978), Ollivier-Pierre (1980), Plaziat (1981) and Pomerol (1973).

non-marine in the Rhine Graben (Sittler 1969) and it seems unlikely that it could then have formed a physical barrier to the spread of faunas from the north-west.

The English Bartonian mammals, except for the Barton and Creechbarrow endemics, must have reached the sites by means of an interchange with continental Europe. Heavy mineral evidence suggests that a land bridge from Dorset to the Cotentin peninsula existed in the Auversian (Morton 1982, i.e. top of his unit 7). It has also been suggested that the Weald–Artois Axis was active at this time (Pomerol 1973) and that a land bridge existed here between Britain and the continent during the later Bartonian. No direct evidence exists, owing to erosion of

Palaeogene sediments in the London Basin. Typical Barton Clay mollusc faunas, which might be expected to occur, are absent from Belgium to the east of the supposed bridge. The presence of continental European mammal species in the English later Bartonian strongly supports the presence of an at least intermittent Weald–Artois or Dorset–Cotentin land bridge. See Text-fig. 71 for palaeogeographic map of Europe in the Bartonian.

Migrations after the Bartonian. Schmidt-Kittler (1977*b*) thought that the primitive *Treposciurus* and *Suevosciurus*, being common to all provinces in the Ludian, may have represented 'relics of an earlier fauna common throughout Europe'. However, they are unknown in pre-Ludian deposits except at Creechbarrow. It is more likely therefore that they are differentiated in the northern area and intermittently spread southwards. *Treposciurus* was first, appearing in the early Ludian of Eclépens B, Fons 4 and Roc de Santa. *Suevosciurus* came later in the late Ludian of Entreroches and Escamps and the middle Oligocene of Armissan. Whether these genera were already in Bavaria before the Ludian is unclear. *Heterohyus morinionensis* may also have originated in the north and spread south, giving rise to *H. quercyi* of the French Ludian. *Leptadapis magnus* (including aff.) is not recorded from pre-Ludian strata except at Creechbarrow, but some lower molars from old Quercy collections with similar primitive morphology to those from Creechbarrow may be Bartonian.

Newcomers to the English early Ludian (for faunal lists, see Hooker & Insole, 1980) from the south are more numerous, e.g. *Isoptychus*, *Plagiolophus annectens*, *Pseudoloris parvulus*, *Quercygale angustidens*, *Gesneropithex* aff. *grisollensis*, *Gliravus*, *Catodontherium* and *Anchilophus*. English Ludian descendants of known English or northern endemic Bartonian taxa are restricted to *Scraeva* spp., *Treposciurus* spp., *Suevosciurus* sp. and *Microchoerus* spp., the list including genera that also spread southwards.

The mammalian fauna at the base of the Lower Headon Beds, including its newcomers of uncertain provenance, is thus very different from that which went before. It is dominated by semi-hypsodont theridomyids, palaeotheriids and artiodactyls, at the expense of the more brachyodont taxa, especially pseudosciurids, paramyids, lophiodontids, apatemyids and paroxyclaenids, which became either reduced in abundance and diversity or extinct. Certain little-modified surviving genera often show trends from frugivory towards folivory (e.g. *Microchoerus*).

This sudden faunal turnover is more likely to represent extinction and migration in relation to some important environmental change than an evolutionary jump. Such a turnover may be a critical point reaction to the more gradual floristic changes suggested by Collinson *et al.* (1981) in the Hampshire Basin coastal area in the late Eocene. Penecontemporaneous changes of a similar degree and nature occur in the mammalian faunas of southern France (Garimond *et al.* 1975), suggesting that the environmental change was on a European scale.

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References

Alston, E. R. 1876. On the classification of the order Glires. *Proc. zool. Soc. Lond.*, **1876:** 61–98, pl. 4.

Anadón, P. & Zamarreño, I. 1981. Paleogene nonmarine algal deposits of the Ebro Basin, northeastern Spain. *In* Monty, C. (ed.), *Phanerozoic Stromatolites*: 140–154, 4 pls, 2 figs. Berlin, Heidelberg, New York.

Andrews, C. W. 1907. Note on the cervical vertebra of a *Zeuglodon* from the Barton Clay of Barton Cliff (Hampshire). *Q. Jl geol. Soc. Lond.*, **63:** 124–127, 1 fig.

Arkell, W. J. 1947. The Geology of the Country around Weymouth, Swanage, Corfe and Lulworth. xix + 386 pp., 19 pls, 84 figs. *Mem. geol. Surv. U.K.*, London.

Astre, G. 1960. Quelques variants extrêmes chez Lophiodon. *Bull. Soc. Hist. nat. Toulouse*, **95** (3/4): 213–224, 2 figs.

Aubry, M.-P. 1983. Biostratigraphie du Paléogène épicontinental de l'Europe du Nord-Ouest. Étude fondée sur les nannofossiles calcaires. *Docums Lab. Géol. Fac. Sci. Lyon*, **89.** 317 pp., 38 figs, 8 pls, 7 tabs.

Aymard, A. 1846. Essai monographique sur un genre nouveau de mammifère fossile trouvé dans la Haute-Loire et nommé *Entelodon*. *Annls Soc. Agric. Sci. Puy*, **12:** 227–267, 1 pl.

—— 1850. (Réponse à M. Robert.) *Annls Soc. Agric. Sci. Puy*, **14:** 80–86.

Azzaroli, A. 1981. Cainozoic mammals and the biostratigraphy of the island of Sardinia, Western Mediterranean. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **36:** 107–111, 1 fig.

Beaumont, G. de 1966. Les Miacinae (Carnivora, Miacidae) de l'Eocène de la Suisse. *Bull. Soc. vaud. Sci. nat.*, Lausanne, **69** (6): 273–285, 1 pl., 2 figs.

Bell, D. L. & Goodell, H. G. 1967. A comparative study of glauconite and the associated clay fraction in modern marine sediments. *Sedimentology*, Amsterdam, New York, **9:** 169–202.

Black, C. C. 1968. The Oligocene rodent *Ischyromys* and discussion of the family Ischyromyidae. *Ann. Carneg. Mus.*, Pittsburgh, **39** (18): 273–305, 26 figs, 3 tabs.

—— 1971. Paleontology and geology of the Badwater Creek Area, Central Wyoming. Part 7, Rodents of the family Ischyromyidae. *Ann. Carneg. Mus.*, Pittsburg, **43** (6): 179–217, 73 figs, 2 tabs.

Blainville, H. M. D. de 1864 (1839–64). *Ostéographie, ou Description Iconographique composée du Squelette et du Système dentaire de Mammifères récents et fossiles pour Servir de base à la zoologie ou à la géologie.* 8 vols, Paris.

Blissenbach, E. 1954. Geology of alluvial fans in semi-arid regions. *Bull. geol. Soc. Am.*, New York, **65:** 175–190.

Blondeau, A. & Pomerol, C. 1969. A contribution to the sedimentological study of the Palaeogene of England. *Proc. Geol. Ass.*, London, **79** (4): 441–455, 4 figs.

Bloomfield, A. H. 1911. Bembridge fossils on Creechbarrow Hill, Isle of Purbeck. *Geol. Mag.*, London, (5) **8** (1): 46.

—— 1913. Bembridge Limestone at Creechbarrow Hill. *Geol. Mag.*, London, (5) **10:** 45–46, 1 fig.

Blumenbach, J. F. 1779. *Handbuch der Naturgeschichte*, **1**. 448 pp., 2 pls. Göttingen.

Boccaletti, M. & Manetti, P. 1978. The Tyrrhenian Sea and adjoining regions. *In* Nairn, A. E. M., Kanes, W. H. & Stehli, F. C. (eds), *The Ocean Basins and Margins*, **4B:** 149–199. New York.

Bonaparte, C.-L. 1850. 1. Conspectus Systematis Mastozoologiae – Editio altera reformata. *In: Conspectus Systematum.* 4 charts, Leiden.

Bonnichsen, R. 1979. Pleistocene bone technology in the Beringian refugium. *Pap. archaeol. Surv. Canada*, Ottawa, (Mercury ser.) **89.** xiii + 297 pp.

Bosco, C. 1902. Il *Lophiodon sardus* delle ligniti di Terras de Collu (Sardegna). *Atti Accad. naz. Lincei Rc.*, Rome, (5) **11** (2nd Sem.): 178–182, 3 figs.

Bosma, A. A. 1974. Rodent biostratigraphy of the Eocene–Oligocene transitional strata of the Isle of Wight. *Utrecht micropaleont. Bull. spec. Publs*, **1.** 128 pp., 7 pls, 36 figs.

— **& Insole, A. N.** 1976. Pseudosciuridae (Rodentia, Mammalia) from the Osborne Beds (Headonian), Isle of Wight, England. *Proc. K. ned. Akad. Wet.*, Amsterdam, (B) **79:** 1–8, 1 pl.

Bowdich, T. E. 1821. *An Analysis of the natural classifications of Mammalia, for the use of Students and Travellers.* 115 pp., 15 pls. Paris.

Bown, T. M. & Schankler, D. 1982. A review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene), Bighorn Basin, Wyoming. *Bull. U.S. geol. Surv.*, Washington, **1523:** 1–79, 10 pls, 18 figs, 8 tabs.

Bravard, A. 1850. Notes sur les ossements fossiles de Débruge. *In* Gervais, P., *Zoologie et Paléontologie françaises* ... (etc.), **2** (Explication des planches et divers mémoires) expl. pls 46–48: 2–3. Paris. (See Gervais 1852).

Brisson, M. J. 1762. *Regnum animale in classes IX. distributum, sive synopsis methodica.* Editio altera auctior. (viii +) 296 pp. Leiden.

Brunet, M. & Gabilly, J. 1981. Découverte d'une faune de Vertébrés bartoniens dans le Tertiaire continental du Seuil du Poitou. *Bull. Soc. géol. Fr.*, Paris, (7) **23** (1): 95–100, 1 pl.

Buchardt, B. 1978. Oxygen isotope palaeotemperatures from the Tertiary Period in the North Sea area. *Nature, Lond.*, **275:** 121–123, 2 figs.

Bujak, J. P., Downie, C., Eaton, G. L. & Williams, G. L. 1980. Dinoflagellate cysts and acritarchs from the Eocene of southern England. *Spec. Pap. Palaeont.*, London, **24:** 1–100, 22 pls, 24 figs.

Burton, E. St J. 1929. The Horizons of Bryozoa (Polyzoa) in the Upper Eocene Beds of Hampshire. *Q. Jl geol. Soc. Lond.*, **85:** 223–239.

—— 1933. Faunal horizons of the Barton Beds in Hampshire. *Proc. Geol. Ass.*, London, **44:** 131–167.

Bury, H. 1934. "Creech Barrow". *Proc. Bournemouth nat. Sci. Soc.*, **26:** 68–72.

Butler, P. M. 1939. Studies of the mammalian dentition. Differentiation of the postcanine dentition. *Proc. zool. Soc. Lond.*, **109:** 1–36.

—— 1947. An Arctocyonid from the English Ludian. *Ann. Mag. nat. Hist.*, London, (11) **13** (106): 691–701, 2 figs.

—— 1952*a*. The milk-molars of Perissodactyla, with remarks on molar occlusion. *Proc. zool. Soc. Lond.*, **121** (4): 777–817, 16 figs.

—— 1952*b*. Molarisation of the premolars in the Perissodactyla. *Proc. zool. Soc. Lond.*, **121** (4): 819–843, 93 figs.

—— 1956. The skull of *Ictops* and the classification of the Insectivora. *Proc. zool. Soc. Lond.*, **126** (3): 453–481, 8 figs.

—— 1967. Dental merism and tooth development. *J. dent. Res.*, Baltimore, **46:** 845–850.

—— 1972. The problem of insectivore classification. *In* Joysey, K. A. & Kemp, T. S., *Studies in Vertebrate Evolution*: 253–265, 6 figs. Edinburgh.

—— 1980. Functional aspects of the evolution of rodent molars. *Palaeovertebrata*, Montpellier, **Mem. jub. Lavocat:** 249–262, 7 figs.

Cartmill, M. 1974. *Daubentonia*, *Dactylopsila*, woodpeckers and klinorhynchy. *In* Martin, R. D., Doyle, G. A. & Walker, A. C., *Prosimian Biology*: 655–670, 5 figs, 2 tabs. London.

Casanovas-Cladellas, M. L. 1975. Estratigraphía y Paleontología del yacimiento ludiense de Roc de Santa (area del Noguera–Pallaresa). *Paleont. Evoluc.*, Sabadell, **10:** 1–158, 11 pls, 12 figs, 28 tabs.

Cavelier, C. 1979. La limite Eocène–Oligocène en Europe occidentale. *Sci. géol. Inst. Géol. Strasbourg* (Mém.) **54:** 1–280, 6 figs, 40 tabs.

—— 1980. Ludien. *In* Cavelier, C. & Roger, J., Les étages français et leurs stratotypes. *Mém. Bur. Rech. géol. minièr.*, Paris, **109:** 237–244.

—— **& Pomerol, C.** 1976. Les rapports entre le Bartonien et le Priabonien. Incidence sur la position de la limite Eocène moyen–Eocène supérieur. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1976** (2): 49–51, 1 tab.

Chamberlain, C. K. 1975. Recent lebensspuren in nonmarine aquatic environments. *In* Frey, R. W. (ed.), *The Study of Trace Fossils. A synthesis of Principles, Problems and Procedures in Ichnology*: 431–458, 10 figs. Berlin, Heidelberg, New York.

Chandler, M. E. J. 1960. Plant remains of the Hengistbury and Barton Beds. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **4:** 191–238, pls 29–35.

—— 1964. A summary and survey of findings in the light of recent botanical observations. *The Lower Tertiary Floras of Southern England*, **4**. xii + 151 pp., 6 figs, 4 pls. London, British Museum (Natural History).

—— 1978. Supplement to the Lower Tertiary floras of Southern England, part 5. *Tert. Res. spec. Pap.*, London, **4**. iv + 47 pp., 20 pls, 6 figs.

Chantre, E. & Gaillard, C. 1897. Sur la faune du gisement sidérolithique éocène de Lissieu (Rhône). *C.r. hebd. Séanc. Acad. Sci.*, Paris, **125:** 986–987.

Châteauneuf, J.-J. 1980. Palynostratigraphie et paléoclimatologie de l'Eocène supérieur et de l'Oligocène du Bassin de Paris (France). *Mém. Bur. Rech. géol. minièr.*, Paris, **116:** 1–357, 31 pls.

Chow Minchen 1964. A lemuroid primate from the Eocene of Lantian, Shensi. *Vertebr. palasiat.*, Peking, **8:** 257–262, 1 pl. [In Chinese and English].

Clarke, M. R. 1981. The sand and gravel resources of the country north of Bournemouth, Dorset. *Miner. Assess. Rep. Inst. geol. Sci.*, London, **51**. iii + 128 pp., 12 figs, 1 pl.

Clemens, W. A. 1966. Fossil Mammals of the Type Lance Formation, Wyoming. Part 2, Marsupialia. *Univ. Calif. Publs geol. Sci.*, Berkeley, **62**. vi + 122 pp., 77 figs, 24 tabs.

—— 1979. Marsupialia. *In* Lillegraven, J. A., Kielan-Jaworowska, Z. & Clemens, W. A. (eds), *Mesozoic Mammals, the first two thirds of mammalian history*: 192–220, 7 figs. Berkeley, Los Angeles, London.

Collinson, M. E. 1983. Palaeofloristic assemblages and palaeoecology of the Lower Oligocene Bembridge Marls, Hamstead Ledge, Isle of Wight. *Bot. J. Linn. Soc.*, London, **86:** 177–225, 68 figs.

—— **, Fowler, K. & Boulter, M.** 1981. Floristic changes indicate a cooling climate in the Eocene of southern England. *Nature, Lond.*, **291:** 315–317, 2 figs.

Coombs, W. P., jr & Coombs, M. C. 1977. The origin of anthracotheres. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **1977** (10): 584–599, 5 figs.

Cooper, C. F. 1910. *Microchoerus erinaceus* (Wood). *Ann. Mag. nat. Hist.*, London, (8) **6:** 39–43, pl. 3.

—— 1928. *Pseudamphimeryx hantonensis*, sp. n., with notes on certain species of artiodactyls from the Eocene deposits of Hordwell. *Ann Mag. nat. Hist.*, London, (10) **2:** 49–55, pls 2–3.

Cooper, J. 1976. British Tertiary Stratigraphical and Rock terms formal and informal, additional to Curry 1958, *Lexique Stratigraphique International. Tert. Res. spec. Pap.*, London, **1:** 1–37.

Cope, E. D. 1867. An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct *Cetacea* of the United States. *Proc. Acad. nat. Sci. Philad.*, **1867:** 138–156.

—— 1873. Third account of new Vertebrata from the Bridger Eocene of Wyoming Territory. *Proc. Am. phil. Soc.*, Philadelphia, **12:** 469–472.

—— 1880. On the genera of the Creodonta. *Proc. Am. phil. Soc.*, Philadelphia, **19:** 76–82.

—— 1881. A new type of Perissodactyla. *Am. Nat.*, Salem, **15:** 1017–1018.

—— 1883. The extinct Rodentia of North America. *Am. Nat.*, Salem, **17:** 43–57, 165–174, 370–381.

—— 1884. The Vertebrata of the Tertiary formations of the West. *Rep. U.S. geol. Surv. Territ.*, Washington, (F. V. Hayden) **3:** 1–1009, Atlas pls 1–75a.

—— 1889. The Vertebrata of the Swift Current River, II. *Am. Nat.*, Salem, **23:** 151–155.

Costa, L. I., Downie, C. & Eaton, G. L. 1976. Palynostratigraphy of some Middle Eocene sections from the Hampshire Basin (England). *Proc. Geol. Ass.*, London, **87** (3): 273–284, 3 figs, 1 tab.

Cox, L. R. 1954. Obituary notice – Arthur George Wrigley. *Proc. malac. Soc. Lond.*, **30** (6): 157–160.

Cray, P. E. 1973. Marsupialia, Insectivora, Primates, Creodonta and Carnivora from the Headon Beds (Upper Eocene) of southern England. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **23** (1): 1–102, 6 pls, 23 figs, 18 tabs.

Creighton, G. K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. *J. Zool., Lond.*, **191:** 435–443, 2 figs.

Crochet, J.-Y. 1977. Les Didelphidae (Marsupicarnivora, Marsupialia) holarctiques tertiaires. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **284:** 357–360, 1 pl.

—— 1979. Diversité systématique des Didelphidae (Marsupialia) européens tertiaires. *Géobios*, Lyon, **12** (3): 365–368, 16 text-figs.

—— 1980. *Les Marsupiaux du Tertiaire d'Europe*. 279 pp., 2 pls, 241 figs, 40 tabs. Paris (Edns Fond. Singer-Polignac).

—— **, Hartenberger, J.-L., Rage, J.-C., Remy, J. A., Sigé, B., Sudre, J. & Vianey-Liaud, M.** 1981. Les nouvelles faunes de vertébrés antérieurs à la 'Grande Coupure' découvertes dans les phosphorites du Quercy. *Bull. Mus. natn. Hist. nat., Paris*, (4) **3** (C, Sci. terre) (3): 245–266.

Crusafont-Pairo, M. 1967. Sur quelques prosimiens de l'Eocène de la zone préaxiale pyrénaïque et un essai provisoire de réclassification. *Colloques int. Cent. natn. Rech. scient.*, Paris, Problèmes actuels de Paléontologie – Evolution des Vertébrés, no. **163:** 611–632.

—— **& Golpe-Posse, J. M.** 1975. Les prosimiens de la région préaxiale pyrénaïque. II Adapidae. *Colloques int. Cent. natn. Rech. scient.*, Paris, Problèmes actuels de Paléontologie – Evolution des Vertébrés, no. **218:** 851–859, 3 figs, 1 pl.

—— **& Russell, D. E.** 1967. Un nouveau Paroxyclaenidé de l'Eocène d'Espagne. *Bull. Mus. natn. Hist. nat. Paris*, (2) **38:** 757–773.

Curry, D. 1937. The English Bartonian Nummulites. *Proc. Geol. Ass.*, London, **48:** 229–246, 2 pls.

—— 1942. The Eocene succession at Afton Brickyard, I.O.W. *Proc. Geol. Ass.*, London, **53** (2): 88–101, pl. 3.

—— 1958*a*. Angleterre, Pays de Galles, Ecosse. Paléogène. *Lexique Strat. Int.*, Paris, **1**, Europe (3a xii). 82 pp.

—— 1958*b*. Itinerary IV. The Barton Area. *In* Curry, D. & Wisden, D. E., The Geology of the Southampton Area. *Geol. Ass. Guide*, Colchester, **14:** 8–12.

—— 1962. Sur la découverte de *Nummulites variolarius* (Lamarck) dans le Lutétien des bassins de Paris et du Hampshire. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1961:** 247.

—— 1967. Problems of correlation in the Anglo–Paris–Belgian Basin. *Proc. Geol. Ass.*, London, **77:** 437–467, 5 figs.

—— 1977. The age of the Hengistbury Beds (Eocene) and its significance for the structure of the area around Christchurch, Dorset. *Proc. Geol. Ass.*, London, **87** (4): 401–407, 2 figs.

—— 1981. Bartonian. *In* Pomerol, C. (ed.), Stratotypes of Paleogene Stages. *Bull. Inf. Géol. Bassin Paris*, (Mém. hors série) **2:** 23–36, 2 figs.

—— **, Adams, C. G., Boulter, M. C., Dilley, F. C., Eames, F. E., Funnell, B. M. & Wells, M. K.** 1978. A correlation of Tertiary rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.* **12**. 72 pp., 5 figs, 2 tabs.

—— **, Daley, B. & Edwards, N.** 1972. Itinerary I, Whitecliff Bay. *In* Curry, D., Daley, B., Edwards, N., Middlemiss, F. A., Stinton, F. C. & Wright, C. W., The Isle of Wight (3rd edn). *Geol. Ass. Guide*, Colchester, **25:** 3–7, figs 2–3.

—— **& Edwards, N.** 1972. Itinerary VIII, Alum Bay and Headon Hill. *In* Curry, D., Daley, B., Edwards, N., Middlemiss, F. A., Stinton, F. C. & Wright, C. W., The Isle of Wight (3rd edn). *Geol. Ass. Guide*, Colchester, **25:** 21–23.

—— **, Hodson, F. & West, I. M.** 1968. The Eocene succession in the Fawley Transmission Tunnel; with an appendix on the clay mineralogy of the strata by R. J. Gilkes. *Proc. Geol. Ass.*, London, **79** (2): 179–206, 6 figs, 1 tab.

—— **, King, A. D., King, C. & Stinton, F. C.** 1977. The Bracklesham Beds (Eocene) of Bracklesham Bay and Selsey, Sussex. *Proc. Geol. Ass.*, London, **88** (4): 243–254, 6 figs.

Cuvier, G. 1804–05. Sur les espèces d'animaux dont proviennent les os fossiles répandus dans la pierre à plâtre des environs de Paris (1–3 mém., 1 sect.). *Annls Mus. Hist. nat. Paris*, **3:** 275–303, 364–387, 442–472, pls 1–13, 1(38)–6(43) (1804). (3 mém., 2 sect.): Restitution des pieds de devant. *Loc. cit.*, **6:** 253–283, pls 1–5(50–54) (1805).

—— 1812. *Recherches sur les ossemens fossiles de quadrupèdes ou l'on rétablit les caractères de plusieurs espèces d'animaux que les révolutions du globe paroissent avoir détruites*, **3**. 394 pp., 68 pls. Paris.

—— 1822. *Recherches sur les ossemens fossiles, où l'on rétablit les caracteres de plusieurs animaux, dont les révolutions du globe ont détruit les espèces.* (New edn), **2**. 648 pp., 60 pls. **3**. 412 pp., 80 pls. Paris.

Daley, B. 1972*a*. Macroinvertebrate assemblages from the Bembridge Marls (Oligocene) of the Isle of Wight, England, and their environmental significance. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **11:** 11–32, 4 figs, 2 tabs.

—— 1972*b*. Some problems concerning the early Tertiary climate of southern Britain. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **11:** 177–190.

—— 1974. Shell encrusting Algae from the Bembridge Marls (Lattorfian) of the Isle of Wight, Hampshire, England. *Revue Micropaléont.*, Paris, **17** (1): 15–22, 3 pls.

—— **& Edwards, N.** 1971. Palaeogene warping in the Isle of Wight. *Geol. Mag.*, London, **108** (5): 399–405, 3 figs.

—— —— **& Insole, A. N.** 1979. Lithostratigraphical nomenclature of the English Palaeogene succession. *Geol. Mag.*, London, **116** (1): 65–66.

Davis, D. D. 1962. Mammals of the lowland rain-forest of North Borneo. *Bull. natn. Mus. St. Singapore*, **31:** 1–129, 23 pls, 20 figs.

Dearman, W. R. 1964. Wrench faulting in Cornwall and south Devon. *Proc. Geol. Ass.*, London, **74** (3): 265–287, 5 figs.

Dechaseaux, C. 1965. Artiodactyles des Phosphorites du Quercy. 1. Étude sur le genre *Dichodon*. *Annls*

Paléont., Paris, (Vert.) **51** (2): 91–108, 8 figs.

Decker, R. L. & Szalay, F. S. 1974. Origins and function of the pes in the Eocene Adapidae (Lemuriformes, Primates). *In* Jenkins, F. A. jr., *Primate Locomotion*: 261–291, 11 figs. New York, London.

Dedieu, P. 1977. Sur la Systématique des Tapiroidea (Mammalia) de l'Eocène européen. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **284** (22): 2219–2222, 1 fig.

Dehm, R. 1937. Über die altertiäre Nager Familie Pseudosciuridae und ihr Entwicklung. *Neues Jb. Miner. Geol. Paläont. BeilBd.*, Stuttgart, (B) **77**: 268–290.

—— 1970. Zur Bezeichnung fossil führender Spaltenfüllungen. *Mitt. bayer. St. Paläont. Hist. Geol.*, München, **10**: 351–364, 1 fig.

Depéret, C. 1894. Sur un gisement sidérolithique de mammifères de l'Eocène moyen, à Lissieu, près Lyon. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **118**: 822–823.

—— 1901. Révision des formes européennes de la famille des Hyracothéridés. *Bull. Soc. géol. Fr.*, Paris, (4) **1**: 199–225, pls 4–5.

—— 1906. Sur une nouvelle espèce de *Lophiodon* (*L. Thomasi*) du Bartonien de Sergy (Aisne). *Bull. Soc. géol. Fr.*, Paris, (4) **6**: 688–692, 1 fig.

—— 1908. L'histoire géologique et la phylogénie des anthracothériidés. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **146**: 158–162.

—— 1910. Etudes sur la famille des Lophiodontidés. *Bull. Soc. géol. Fr.*, Paris, (4) **10**: 558–577, pl. 7.

—— 1917. Monographie de la faune de mammifères fossiles du Ludien inférieur d'Euzet-les-Bains (Gard). *Annls Univ. Lyon*, (1) **40**: 1–290, pls 1–25.

—— **& Carrière, G.** 1901. Sur un nouveau gisement de mammifères de l'Eocène moyen à Robiac, près Saint-Mamert (Gard). *C.r. hebd. Séanc. Acad. Sci.*, Paris, **133**: 616–618.

Desmarest, A. G. 1822. *Mammalogie, ou description des espèces de mammifères*, **2**: i–viii, 277–555. Paris.

Dobson, G. E. 1875. Conspectus of the suborders, families and genera of Chiroptera arranged according to their natural affinities. *Ann. Mag. nat. Hist.*, London, (4) **16**: 345–357.

Dorr, J. A. 1977. Partial skull of *Paleosinopa simpsoni* (Mammalia, Insectivora), latest Paleocene Hoback Formation, Central Western Wyoming, with some general remarks on the family Pantolestidae. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **24** (23): 281–307, 5 figs.

Drummond, P. V. O. 1970. The Mid-Dorset Swell. Evidence of Albian–Cenomanian movements in Wessex. *Proc. Geol. Ass.*, London, **81**: 679–714.

Eaton, G. L. 1976. Dinoflagellate cysts from the Bracklesham Beds (Eocene) of the Isle of Wight, southern England. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **26** (6): 225–332, 31 figs, 21 pls.

Edwards, F. E. 1852. A Monograph of the Mollusca from the Eocene Formations of England. Part II, Pulmonata. *Palaeontogr. Soc. (Monogr.)*, London: 57–122, pls 10–15.

Eisenberg, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. *In* Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*: 135–152, 6 figs, 6 tabs. Washington D.C., Symp. natn. zool. Park, Smithson. Instn.

Elliott, G. F. 1954. New Brachiopoda from the Eocene of England, France and Africa. *Ann. Mag. nat. Hist.*, London, (12) **7**: 721–728, pl. 15.

Engesser, B., Matter, A. & Weidmann, M. 1981. Stratigraphie und säugetierfaunen des mittleren Miozäns von Vermes (Kt. Jura). *Eclog. geol. Helv.*, Lausanne, Basel, **74** (3): 893–952, 29 figs, 1 tab.

Fahlbusch, V. 1976. Report on the International Symposium on mammalian stratigraphy of the European Tertiary. *Newsl. Stratigr.*, Leiden, **5** (2/3): 160–167, 1 tab.

Feuillée, P. 1964. Historique de l'utilisation du terme 'Bartonien' dans le Bassin de Paris. *Mém. Bur. Rech. géol. minièr.*, Paris, **28**: 37–46.

Filhol, H. 1873. Sur un nouveau genre de lémurien fossile, récemment découvert dans les gisements de phosphate de chaux du Quercy. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **77**: 1111–1112.

—— 1874. Nouvelles observations sur les mammifères des gisements de phosphate de chaux (Lémuriens et pachylémuriens). *Annls Sci. géol. Paris*, **5** (4): 1–36, pls 7–8.

—— 1876–77. Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y recontre et spécialement des mammifères. 1. *Annls Sci. géol. Paris*, **7** (7): 1–220, pls 10–36 (1876*a*). 2. *Loc. cit.* **8** (1): 1–338, pls 1–28 (1877*b*). Also: 1. *Bibltque Ec. ht. Etud., Paris Sect. Sci. nat.*, **15** (4): 1–220, pls 6–32 (1876*a*). 2. *Loc. cit.* **16** (1): 1–338, pls 1–28 (1877*b*). 1 + 2. *Thèse pres. à Fac. Sci. Paris* (&c.). 561 pp., 55 pls. Paris (1877*c*).

—— 1876*b*. Mammifères fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **82**: 288–289.

—— 1877*a*. Considérations sur la découverte de quelques mammifères fossiles appartenant a l'époque éocène supérieure. *Bull. Soc. philomath. Paris*, **7** (1): 51–54.

—— 1877*b*, 1877*c*. See 1876–77.

—— 1879. Étude des mammifères fossiles de St-Gérand-le-Puy. *Bibltque Éc. ht. Étud., Paris Sect. Sci. nat.*, **19** (1): 1–252, 30 pls.

—— 1880*a*. Note sur des mammifères fossiles nouveaux provenant des phosphorites du Quercy. *Bull. Soc. philomath. Paris*, **7** (4): 120–125.

—— 1880*b*. Sur la découverte de mammifères nouveaux dans les dépôts de phosphate de chaux du Quercy. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **90:** 1579–1580.

—— 1882. Mémoires rélatifs à quelques mammifères fossiles provenant des dépôts de phosphorite du Quercy. *Bull. Soc. Sci. phys. nat. Toulouse*, **5** (1): 19–156, pls 1–10.

—— 1884. Observations rélatives à des mammifères fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. *Bull. Soc. Sci. phys. nat. Toulouse*, **5** (2): 159–203, pls 1–13.

—— 1888*a*. Etude sur les vertébrés fossiles d'Issel (Aude). *Mém. Soc. géol. Fr.*, Paris, (3) **5** (1): 1–188, 21 pls.

—— 1888*b*. Description d'un nouveau genre de Pachyderme provenant des dépôts de phosphate de chaux du Quercy. *Bull. Soc. philomath. Paris*, (7) **12** (4): 143–147.

—— 1890*a*. Description d'un nouveau genre de mammifère. *Bull. Soc. philomath. Paris*, **8** (2): 34–38, 1 fig.

—— 1890*b*. Description d'une nouvelle espèce de Lémurien fossile. *Bull. Soc. philomath. Paris*, (8) **2:** 39–40.

—— 1890*c*. Description d'un nouveau genre d'insectivore. *Bull. Soc. philomath. Paris*, (8) **2** (4): 174–175, 3 figs.

Fischer, J. B. 1829. *Synopsis Mammalium.* xlii + 752 pp., 4 tabs. Stuttgart.

Fischer, K.-H. 1964. Die tapiroiden Perissodactylen aus der eozänen Braunkohle des Geiseltales. *Geologie*, Berlin, **45:** 1–101, 22 figs, 10 pls.

—— 1977. Neue Funde von *Rhinocerolophiodon* (n. gen.), *Lophiodon* und *Hyrachyus* (Ceratomorpha, Perissodactyla, Mammalia) aus dem Eozän des Geiseltals bei Halle (DDR). 1 Teil: *Rhinocerolophiodon. Z. geol. Wiss.*, Berlin, **5** (7): 909–919, 5 figs (1977*a*). 2 Teil: *Lophiodon. Loc. cit.*, **5** (9): 1129–1152, 18 figs (1977*b*).

Fisher, D. C. 1981*a*. Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth. *Paleobiology*, Chicago, **7** (2): 262–275, 4 figs.

—— 1981*b*. Taphonomic interpretation of enamel-less teeth in the Shotgun local fauna (Paleocene, Wyoming). *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **25** (13): 259–275, 4 figs.

Fisher, O. 1862. On the Bracklesham Beds of the Isle of Wight Basin. *Q. Jl geol. Soc. Lond.*, **18:** 65–94, 4 figs.

Fitch, F. J., Hooker, P. J., Miller, J. A. & Brereton, N. R. 1978. Glauconite dating of Palaeocene–Eocene rocks from East Kent and the time scale of Palaeogene volcanism in the North Atlantic region. *J. geol. Soc. Lond.*, **135:** 499–512, 14 figs, 2 tabs.

Flower, W. H. 1883. On the arrangement of the orders and families of existing Mammalia. *Proc. zool. Soc. Lond.*, **1883:** 178–186.

—— 1884. *Catalogue of the specimens illustrating the osteology and dentition of vertebrated animals, recent and extinct, contained in the Museum of the Royal College of Surgeons of England.* **2,** Mammalia other than man. xliii + 779 pp. London.

Flügel, E. 1964. Microproblematica aus den rhätischen Riffkalken der Nordalpen. *Paläont. Z.*, Berlin, **38** (1/2): 74–87, 1 tab., 1 fig., pls 8–9.

Flynn, J. J. & Galiano, H. 1982. Phylogeny of early Tertiary Carnivora, with a description of a new species of *Protictis* from the middle Eocene of northwestern Wyoming. *Am. Mus. Novit.*, New York, **2725:** 1–64, 9 figs, 2 tabs.

Fogden, M. P. L. 1974. A preliminary field study of the western tarsier, *Tarsius bancanus* Horsefield. *In* Martin, R. D., Doyle, G. A. & Walker, A. C., *Prosimian Biology*: 151–165, 4 figs, 1 tab. London.

Fortey, R. A. & Jefferies, R. P. S. 1982. The use of stratigraphy in determining phylogeny, a compromise approach. *In* Joysey, K. A., *Problems of Phylogenetic Reconstruction*: 197–234, 17 figs. London, Spec. Vol. Systs Assn.

Fowler, K., Edwards, N. & Brett, D. W. 1973. *In situ* coniferous (taxodiaceous) tree remains in the upper Eocene of southern England. *Palaeontology*, London, **16** (1): 205–217, pl. 19, 1 fig.

Franzen, J.-L. 1968. *Revision der Gattung Palaeotherium Cuvier 1804 (Palaeotheriidae, Perissodactyla, Mammalia).* **1,** 181 pp., 20 figs; **2,** 35 pls, 15 tabs. Freiburg, Inaugural-Dissertation zur Erlangung der Doktorwürde der Naturwissenschaftlich-matematischen Facultät der Albert-Ludwigs-Universität zu Freiburg i. Br.

—— 1972. *Pseudopalaeotherium longirostratum* n.g., n.sp. (Perissodactyla, Mammalia) aus dem unterstampischen Kalkmergel von Ronzon (Frankreich). *Senckenberg. leth.*, Frankfurt a.M., **53** (5):

315–331, 8 figs, 2 tabs.

—— 1980*a*. *In* Franzen, J. L. & Krumbiegel, G., *Messelobunodon ceciliensis* n. sp. (Mammalia, Artiodactyla), ein neuer Dichobunide aus der mitteleocänen Fauna des Geiseltales bei Halle (D.D.R.). *Z. geol. Wiss.*, Berlin, **8** (12): 1585–1592, 3 figs, 1 pl.

—— 1980*b*. Das Skelett eines juvenilen Propalaeotherium isselanum (Mammalia, Equidae) aus dem mitteleozänen Ölschiefer der Grube Messel bei Darmstadt. *Dortmund. Beitr. Landeskde*, **14:** 85–102, 1 fig., 5 pls, 2 tabs.

—— 1981. Das erste Skelett eines Dichobuniden (Mammalia, Artiodactyla) geborgen aus mitteleozänen Ölschiefern der 'Grube Messel' bei Darmstadt (Deutschland, S-Hessen). *Senckenberg. leth.*, Frankfurt a.M., **61** (3/6): 299–353, 11 figs, 6 tabs, 11 pls.

Freshney, E. C. 1978. Ramnor Inclosure Borehole. *In* Institute of Geological Sciences, I.G.S. boreholes 1977. *Rep. Inst. geol. Sci.*, London, **78** (21): 5–6.

—— **& Edwards, R. A.** 1983. Christchurch borehole. *In* Institute of Geological Sciences, I.G.S. boreholes 1981. *Rep. Inst. geol. Sci.*, London, **82** (11): 1–3.

Gardner, J. S. 1879. Description and correlation of the Bournemouth Beds. Part 1. Upper Marine Series. *Q. Jl geol. Soc. Lond.*, **35:** 209–228, 6 figs.

—— **, Keeping, H. & Monckton, H. W.** 1888. The Upper Eocene, comprising the Barton and Upper Bagshot Formations. *Q. Jl geol. Soc. Lond.*, **44:** 578–635.

Garimond, S., Remy, J. A. & Sudre, J. 1975. Nouvelles données sur le renouvellement des faunes de mammifères à l'Eocène supérieur, d'après les gisements de Fons (Gard). *Colloques int. Cent. natn. Rech. scient.*, Paris, Problèmes actuels de Paléontologie–Evolution des vertébrés, no. **218:** 611–625, 7 figs, 3 tabs.

Gaudant, J. 1979. Sur la présence de dents de Characidae (poissons teléostéens, Ostariophysi) dans les 'Calcaires à Bithynies' et les 'Sables Bleutés' du Var. *Géobios*, Lyon, **12** (3): 451–457, 1 fig., 1 pl.

Gervais, P. 1849. Recherches sur les mammifères fossiles des genres *Palaeotherium* et *Lophiodon*, et sur les autres animaux de la même classe que l'on a trouvés avec eux dans le midi de la France. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **29:** 381–384.

—— 1850. Nouvelles recherches relatives aux mammifères d'espèces éteintes qui sont enfouies auprès d'Apt, avec des *Paleotheriums* identiques à ceux de Paris. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **30:** 602–604.

—— 1852 (1848–52). *Zoologie et Paléontologie françaises (animaux vertébrés) ou Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France.* 1st edn. **1** (text), 271 pp.; **2** (pl. expl.); **3** (atlas), 80 pls. Paris. See 1859.

—— 1856. Sur les mammifères fossiles que l'on a recueillis dans le département du Gard. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **42:** 1159–1161.

—— 1859. *Zoologie et Paléontologie françaises* ... (&c.). 2nd edn. **1** (text), viii + 544 pp., 51 figs; **2** (atlas), xii + 84 pls. Paris.

—— 1875. *Palaeothérium* du calcaire grossier. *J. Zool., Paris*, **4:** 421–422.

—— 1876. *Zoologie et Paléontologie générales, nouvelles recherches sur les Animaux Vertébrés dont on trouve les ossements enfouis dans le sol et sur leur comparaison avec les espèces actuellement existantes.* 2nd edn. 72 pp., 25 pls. Paris.

Gilkes, R. J. 1968. Clay mineral provinces in the Tertiary sediments of the Hampshire Basin. *Clay Miner.*, Oxford, **7:** 351–361, 3 figs, 1 pl.

—— 1978. On the clay mineralogy of upper Eocene and Oligocene sediments in the Hampshire Basin. *Proc. Geol. Ass.* London, **89:** 43–56, 7 figs.

Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithson. misc. Collns*, Washington, **11** (230, Art. 1). vi + 98 pp.

Gingerich, P. D. 1972. Molar Occlusion and Jaw Mechanics of the Eocene Primate *Adapis*. *Am. J. phys. Anthrop.*, Washington, **36** (3): 359–368, 8 figs.

—— 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *J. Paleont.*, Tulsa, **48:** 895–903.

—— 1975*a*. Systematic position of *Plesiadapis*. *Nature, Lond.*, **253** (5487): 111–113, 2 figs.

—— 1975*b*. Dentition of *Adapis parisiensis* and the Evolution of Lemuriform Primates. *In* Tattersall, I. & Sussman, R. W. (eds), *Lemur Biology*: 65–80, 8 figs. New York.

—— 1975*c*. A new genus of Adapidae (Mammalia, Primates) from the late Eocene of southern France, and its significance for the origin of higher primates. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **24** (15): 163–170, 3 figs.

—— 1976*a*. Paleontology and phylogeny: patterns of evolution at the species level in early Tertiary mammals. *Am. J. Sci.*, New Haven, **276:** 1–28.

—— 1976*b*. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Pap.*

Paleont. Mus. Paleont. Univ. Mich., Ann Arbor, **15:** 1–140, 42 figs, 14 + 17 (appendix) tabs, 12 pls.

—— 1977*a*. New species of Eocene primates and the phylogeny of European Adapidae. *Folia Primatol.*, Basel, **28:** 60–80, 8 figs, 2 tabs.

—— 1977*b*. Radiation of Eocene Adapidae in Europe. *Géobios*, Lyon, (Mém. spéc.) **1:** 165–182, 7 figs, 1 tab.

—— 1981. Cranial morphology and adaptations in Eocene Adapidae. 1. Sexual dimorphism in *Adapis magnus* and *Adapis parisiensis*. *Am. J. phys. Anthrop.*, Washington, **56:** 217–234, 8 figs, 3 tabs.

—— 1983. New Adapisoricidae, Pentacodontidae, and Hyopsodontidae (Mammalia, Insectivora and Condylarthra) from the late Paleocene of Wyoming and Colorado. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **26** (11): 227–255, 10 figs.

—— **& Martin, R. D.** 1981. Cranial morphology and adaptations in Eocene Adapidae. 2. The Cambridge skull of *Adapis parisiensis*. *Am. J. phys. Anthrop.*, Washington, **56:** 235–257, 11 figs, 4 tabs.

—— **& Russell, D. E.** 1981. *Pakicetus inachus*, a new archaeocete (Mammalia, Cetacea) from the early–middle Eocene Kuldana Formation of Kohat (Pakistan). *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **25** (11): 235–246, 5 figs.

—— ——, **Sigogneau-Russell, D. & Hartenberger, J.-L.** 1979. *Chorlakkia hassani*, a new middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana Formation of Kohat (Pakistan). *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **25** (6): 117–124, 2 figs, 1 pl.

—— **& Sahni, A.** 1979. *Indraloris* and *Sivaladapis*: Miocene adapid primates from the Siwaliks of India and Pakistan. *Nature, Lond.*, **279** (5712): 415–416, 1 fig., 1 tab.

Ginsburg, L., Arques, J., Broin, F. de, Le Calvez, Y., Mouton, J., Obert, D., Privé-Gill, C. & Roucan, J.-P. 1977. Découverte d'une faune de mammifères dans le Lutétien supérieur de la Défense, à Puteaux, près Paris (Hauts-de-Seine). *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1977** (6): 311–313, 2 figs.

——, **Montenat, C. & Pomerol, C.** 1965. Découverte d'une faune de mammifères terrestres dans les couches marines de l'Auversien (Bartonien inférieur) du Guépelle (Seine-et-Oise). *C.r. hebd. Séanc. Acad. Sci.*, Paris, **260:** 3445–3446.

Godinot, M. 1984. Un nouveau genre témoignant de la diversité des Adapinés (Primates, Adapidae) à l'Eocène terminal. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (II) **299** (18): 1291–1296, 1 pl.

—— 1985. Evolutionary implications of morphological changes in Palaeogene primates. *In* Cope, J. C. W. & Skelton, P. W. (eds), Evolutionary case histories from the fossil record. *Spec. Pap. Palaeont.*, London, **33:** 39–47, 5 figs.

Golpe-Posse, J. M. 1972. Faunas de yacimientos con suiformes en el terciario español. *Paleont. Evoluc.*, Sabadell, **2:** 1–197, appendix 13 pp., 7 pls, 5 figs.

Goudie, A. 1973. *Duricrusts in Tropical Landscapes.* 174 pp., 46 figs. Oxford.

Grambast, L. 1962. Aperçu sur les charophytes tertiaires du Languedoc et leur signification stratigraphique. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1962** (10): 313–314.

—— 1964. Indications fournies par les charophytes pour la stratigraphie du Paléogène. *Mém. Bur. Rech. géol. minièr.*, Paris, **28:** 1009–1011.

—— 1972. Principes de l'utilisation stratigraphique des charophytes. Applications au Paléogène d'Europe occidentale. *Mém. Bur. Rech. géol. minièr.*, Paris, **77:** 319–328, 1 fig.

Grandidier, G. 1904. Un nouveau Lémurien fossile de France, le *Pronycticebus gaudryi*. *Bull. Mus. Hist. nat. Paris*, **10:** 9–13.

Gray, J. E. 1827. Synopsis of the species of the class Mammalia as arranged with reference to their organisation, by Cuvier and other naturalists with specific characters, synonyma etc. *In* Cuvier, G., *The Animal Kingdom arranged in conformity with its organization with additional descriptions of all the species hitherto named, and of many not before noticed, by Edward Griffith and others.* **5,** Mammalia. 391 pp. London.

Gregory, W. K. 1910. The orders of mammals. *Bull. Am. Mus. nat. Hist.*, New York, **27:** 1–254.

—— 1915. On the classification and phylogeny of the Lemuroidea. *Bull. geol. Soc. Am.*, New York, **26:** 426–446.

—— 1920. Studies in comparative myology and osteology, no. 5 – On the anatomy of the preorbital fossae of Equidae and other ungulates. *Bull. Am. Mus. nat. Hist.*, New York, **42** (3): 265–284, pl. 18.

Gruas-Cavagnetto, C. 1970. Aperçu sur la microflore et le microplancton du Paléogène anglais. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1970:** 19–21.

Guth, C. 1964. À propos de *Miacis exilis* des Phosphorites du Quercy. *Mammalia*, Paris, **28** (2): 359–365, pls 15–16, 1 fig.

Haeckel, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Entwicklungsgeschichte der Organismen. Kritische Grundzüge der mechanischen Wissenschaft von den entstehenden formen der Organismen, begründet durch die Descendenz-Theorie.* 2 vols, clx + 462 pp., 8 pls. Berlin.

Halstead, L. B. & Middleton, J. 1972. Notes on fossil whales from the Upper Eocene of Barton, Hampshire. *Proc. Geol. Ass.*, London, **83** (2): 185–190, 3 figs.

Hardenbol, J. & Berggren, W. A. 1978. A new Paleogene numerical time scale. *In* Cohee, G. V., Glaessner, M. F. & Hedberg, H. D., Contributions to the geologic time scale. *Stud. Geol. Am. Assoc. Pet. Geol.*, Tulsa, **6:** 213–234, 8 figs.

Harlan, R. 1834. Notice of fossil bones found in the Tertiary formation of the state of Louisiana. *Trans. Am. phil. Soc.*, Philadelphia, (NS) **4** (3): 397–403, pl. 20.

Harland, W. B. *et al.* 1972. A concise guide to stratigraphical procedure. *J. geol. Soc. Lond.*, **128:** 295 305.

Harpe, P. de la 1869. Sur la faune du terrain sidérolithique dans le canton de Vaud. *Bull. Soc. vaud. Sci. nat.*, Lausanne, **10:** 457–467.

—— **& Gaudin, C.** 1854. Sur les ossements fossiles trouvés par ces messieurs au Mormont, près La Sarraz. *Bull. Soc. vaud. Sci. nat.*, Lausanne, **3** (26): 117–128.

Hartenberger, J.-L. 1968. Les Pseudosciuridae (Rodentia) de l'Eocène moyen et le genre *Masillamys* Tobien. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **267:** 1817–1820.

—— 1969. Les Pseudosciuridae (Mammalia, Rodentia) de l'Eocène moyen de Bouxwiller, Egerkingen et Lissieu. *Palaeovertebrata*, Montpellier, **3** (2): 27–61.

—— 1971. La systématique des Theridomyoidea. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **273:** 1917–1920.

—— 1972. Les mammifères d'Egerkingen et l'histoire des faunes de l'Eocène d'Europe. *Bull. Soc. géol. Fr.*, Paris, (7) **12** (5): 886–893, 1 fig., 2 tabs.

—— 1973. Étude systématique des Theridomyoidea (Rodentia) de l'Eocène supérieur. *Mém. Soc. géol. Fr.*, Paris, (NS) **52** (Mém. 117): 1–76, 8 pls, 20 figs.

—— 1975. Evolution des rongeurs primitifs de l'Ancien Monde. *Colloques int. Cent. natn. Rech. scient.*, Paris, Problèmes actuels de paléontologie – évolution des vertébrés, no. **218:** 777–790, 1 pl., 1 fig., 2 tabs.

—— **& Louis, P.** 1976. Nouveaux rongeurs dans l'Eocène supérieur de Grisolles (Aisne). *Géobios*, Lyon, **9:** 81–95.

—— **& Schmidt-Kittler, N.** 1976. Un nouveau genre de Theridomyoidea (Mammalia, Rodentia) dans les Phosphorites du Quercy. *Mitt. bayer. St. Paläont. Hist. Geol.*, München, **16:** 65–69, 1 pl., 1 fig.

—— **, Sigé, B. & Sudre, J.** 1974. La plus ancienne faune de mammifères du Quercy: Le Bretou. *Palaeovertebrata*, Montpellier, **6:** 177–196, 8 figs, 5 tabs.

Haupt, H. 1956. Beitrag zur Kenntnis der eocänen Arthropodenfauna des Geiseltales. *Nova Acta Leopoldina*, Halle a.S., (NF) **18** (128): 3–90, 106 figs.

Haupt, O. 1921. Die eocänen Süsswasserablagerungen (Messeler Braunkohlenformation) in der Umgegend von Darmstadt und in ihr palaeontologischer Inhalt. *Z. dt. geol. Ges.*, Berlin, **73:** 175-178.

—— 1925. Die Paläohippiden der eocänen Süsswasserablagerungen von Messel bei Darmstadt. *Abh. hess. geol. landesanst.*, Darmstadt, **6** (4): 1–159, 29 pls.

Hay, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bull. U.S. geol. Surv.*, Washington, **179:** i–iii, 1–868.

Hay, R. L. & Reeder, R. J. 1978. Calcretes of Olduvai Gorge and the Ndolanya Beds of northern Tanzania. *Sedimentology*, Amsterdam, New York, **25:** 649–673.

Hedberg, H. (ed.) 1972. Summary of an international guide to stratigraphic classification, terminology, and usage. *Lethaia*, Oslo, **5:** 297–323.

—— (ed.) 1976. *International Stratigraphic Guide: A Guide to Stratigraphic Classification, Terminology, and Procedure.* xvii + 200 pp., 14 figs, 3 tabs. New York, London, Sydney, Toronto.

Heissig, K. 1977. Neues Material von *Cryptopithecus* (Mammalia, Pantolestidae) aus dem Mitteloligozän von "Möhren 13" in Mittelfranken. *Mitt. Bayer. Staatssamml. Paläont. & hist. Geol.*, München, **17:** 213–225, 24 figs.

Heller, F. 1930. Die Säugetierfauna der mitteleozänen Braunkohle des Geiseltales bei Halle a.S. *Jb. halle. Verb. Erforsch. mitteldt. Bodenschätze*, (NF) **9:** 13–41, 5 pls.

—— 1934. *Anthracobunodon weigelti* n.g., n.sp., ein Artiodactyls aus dem Mitteleozän des Geiseltales bei Halle a.S. *Paläont. Z.*, Berlin, **16:** 147–263, 1 fig., 2 pls.

—— 1935. *Amphilemur eocaenicus* n.g. et n.sp., ein primitiver Primate aus dem Mitteleozän des Geiseltales bei Halle a.S. *Nova Acta Leopoldina*, Halle a.S., (NF) **2** (3): 293–300, 1 pl., 1 fig.

—— 1936. Neue Beuteltierreste aus der mitteleozänen Braunkohle des Geiseltales bei Halle (Saale). *Nova Acta Leopoldina*, Halle a.S., (NF) **4:** 311–316, 1 pl.

Hensel, R. 1856. Beiträge zur Kenntnis fossiler Säugetiere. *Z. dt. geol. Ges.*, Berlin, **8:** 660–704.

Hershkovitz, P. 1971. Basic crown patterns and cusp homologies of mammalian teeth. *In* Dahlberg, A. A. (ed.), *Dental Morphology and Evolution*: 95–150, 17 figs. Chicago & London.

Hill, W. C. O. 1953–55. *Primates: Comparative Anatomy and Taxonomy.* **1,** Strepsirhini. xxiii + 798 pp., 34 pls, 199 figs (1953). **2,** Haplorhini. 347 pp., 14 pls (1955). Edinburgh.

Hooke, R. LeB. 1967. Processes on arid-region alluvial fans. *J. Geol.*, Chicago, **75:** 438–460.

Hooker, J. J. 1972. The first land mammals from the marine Barton Beds (Upper Eocene) of Hampshire. *Proc. Geol. Ass.*, London, **83:** 179–184, 1 tab.

— 1975. Report of Field Meeting to Hengistbury Head and adjacent areas, Dorset; with an account of published work and some new exposures. *Tertiary Times*, Bromley, **2** (3): 109–121, 6 figs.

—— 1977*a*. A mammal from the Upper Eocene of Hengistbury, Dorset. *Tert. Res.*, London, **1** (3): 91–94, 1 fig., 1 tab.

—— 1977*b*. The Creechbarrow Limestone – its biota and correlation. *Tert. Res.*, London, **1** (4): 139–145.

—— 1980. The succession of *Hyracotherium* (Perissodactyla, Mammalia) in the English early Eocene. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **33:** 29–42, 6 figs, 1 tab.

—— (1982). *Mammals from the Bartonian (Middle/Late Eocene) of the Hampshire Basin, southern England.* PhD Thesis, Univ. London (unpubl.).

—— 1984. A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe. *Zool. J. Linn. Soc.*, London, **82:** 229–244, 22 figs.

—— **& Insole, A. N.** 1980. The distribution of mammals in the English Palaeogene. *In* Hooker *et al.*, 1980: 31–45, tab. 2. See next ref.

— ——, **Moody, R. T. J., Walker, C. A. & Ward., D. J.** 1980. The distribution of cartilaginous fish, turtles, birds and mammals in the British Palaeogene. *Tert. Res.*, Rotterdam, **3** (1): 1–45, 2 tabs.

—— **& Ward, D. J.** 1980. Introduction and stratigraphy and list of localities. *In* Hooker *et al.* 1980: 1–12, tab. 1. See previous ref.

Hudleston, W. H. 1902–03. Creechbarrow in Purbeck. *Geol. Mag.*, London, NS (4) **9:** 241–256, 4 figs (1902*a*). No. 2. *Loc. cit.* **10:** 149–154, 197–203, pl. 11, 4 figs (1903).

—— 1902*b*. Creechbarrow: an essay in Purbeck geology. *Proc. Dorset nat. Hist. antiq. Fld Club*, Dorchester, **23:** 146–190, 1 pl., 10 figs.

Hürzeler, J. 1946. *Gesneropithex* nov. gen., ein neuer Primate aus dem Ludien von Gösgen (Solothurn). *Verh. schweiz. naturf. Ges.*, Basel, **126:** 126–127.

—— 1947*a*. *Gesneropithex Peyeri* nov. gen. nov. spec., ein neuer Primate aus dem Ludien von Gösgen (Solothurn). *Eclog. geol. Helv.*, Lausanne, Basel, **39** (2): 356–361, 4 figs.

—— 1947*b*. Alsaticopithecus Leemanni nov. gen. nov. spec., ein neuer Primate aus dem unteren Lutétien von Buchsweiler im Unterelsass. *Verh. schweiz. naturf. Ges.*, Basel, **127:** 81–82.

—— 1948*a*. *Alsaticopithecus Leemanni* nov. gen. nov. spec., ein neuer Primate aus dem unteren Lutétien von Buchsweiler im Unterelsass. *Eclog. geol. Helv.*, Lausanne, Basel, **40** (2): 343–356, 12 figs.

—— 1948*b*. Zur Stammesgeschichte der Necrolemuriden. *Abh. schweiz. paläont. Ges.*, Basel, **66:** 1–46, 41 figs, 2 tabs.

Huxley, T. H. 1880. On the application of the laws of evolution to the arràngement of the Vertebrata and more particularly of the Mammalia. *Proc. zool. Soc. Lond.*, **1880:** 649–662.

Illiger, C. 1811. *Prodromus systematis Mammalium et Avium additis terminis zoographicis utriusque classis, eorumque versione Germanica.* xviii + 301 pp. Berlin.

Insole, A. N. (1972). *Upper Eocene and Lower Oligocene Mammal Faunas from Southern England.* PhD Thesis, Univ. Bristol (unpubl.).

International Commission on Zoological Nomenclature 1985. *International Code of Zoological Nomenclature*, 3rd edn. 338 pp. London, Berkeley and Los Angeles.

Jaeger, J.-J. 1971. La faune de mammifères du Lutétien de Bouxwiller (Bas-Rhin) et sa contribution à l'élaboration de l'échelle des zones biochronologiques de l'Eocène européen. *Bull. Serv. Carte géol. Als. Lorr.*, Strasbourg, **24** (2/3): 93–105.

Jepsen, G. L. 1934. A revision of the American Apatemyidae and the description of a new genus, *Sinclairella*, from the White River Oligocene of South Dakota. *Proc. Am. phil. Soc.*, Philadelphia, **74:** 287–305, figs 1–4, pls 1–3.

Jones, F. G. & Wilkinson, B. H. 1978. Structure and growth of lacustrine pisoliths from recent Michigan marl lakes. *J. sedim. Petrol.*, Menasha, **48** (4): 1103–1110, 3 figs.

Kay, R. F. & Cartmill, M. 1977. Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ?Primates), with a description of a new genus and species. *J. hum. Evol.*, London, **6:** 19–53, 10 figs, 1 pl., 5 tabs.

—— **& Hylander, W. L.** 1978. The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). *In* Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*: 173–191, 15 figs. Washington, D.C., Symp. natn. zool. Park, Smithson. Instn.

Keen, M. C. 1977. Ostracod assemblages and the depositional environments of the Headon, Osborne, and Bembridge Beds (upper Eocene) of the Hampshire Basin. *Palaeontology*, London, **20** (2): 405–445, pls

46–49, 11 figs, 2 tabs.

—— 1978. The Tertiary–Palaeogene. *In* Bate, R. & Robinson, E. (eds), A Stratigraphical Index of British Ostracoda. *Geol. J.*, Liverpool, (Spec. Iss.) **8:** 385–450, 8 figs, 12 pls, 5 tabs.

Keeping, H. 1887. On the discovery of the *Nummulina elegans* Zone at Whitecliff Bay, Isle of Wight. *Geol. Mag.*, London, (3) **4:** 70–72.

—— 1910. On the discovery of Bembridge Limestone fossils on Creechbarrow Hill, Isle of Purbeck. *Geol. Mag.*, London, NS (5) **7:** 436–439, 1 fig., pl. 34.

—— 1912. On the results of the further examination of Creechbarrow Hill. *Rep. Br. Ass. Advmt Sci.*, London, (Dundee) **1912:** 129–131.

Kellogg, R. 1936. A review of the Archaeoceti. *Publs Carnegie Instn*, Washington, **482**. xv + 366 pp., 88 figs, 37 pls.

Kemp, D. J., King, A. D., King, C. & Quayle, W. J. 1979. Stratigraphy and biota of the Elmore Formation (Huntingbridge division, Bracklesham Group) at Lee-on-the-Solent, Gosport, Hampshire. *Tert. Res.*, London, **2** (2): 93–103, 5 figs.

Kielan-Jaworowska, Z., Bown, T. M. & Lillegraven, J. A. 1979. Eutheria. *In* Lillegraven, J. A., Kielan-Jaworowska, Z. & Clemens, W. A. (eds), *Mesozoic Mammals, the first two-thirds of mammalian history*: 221–258, 22 figs. Berkeley, Los Angeles, London.

Koenigswald, W. v. 1979. Ein Lemurenrest aus dem eozänen Ölschiefer der Grube Messel bei Darmstadt. *Paläont. Z.*, Berlin, **53:** 63–76, 5 figs.

—— 1980*a*. Das Skelett eines Pantolestiden (Proteutheria, Mammalia) aus dem mittleren Eozän von Messel bei Darmstadt. *Paläont. Z.*, Berlin, **54** (3/4): 267–287, 20 figs, 2 tabs.

—— 1980*b*. Fossillagerstätte Messel – Literaturübersicht der Forschungsergebnisse aus den Jahren 1969–1979. *Geol. Jb. Hessen*, **108:** 23–38, 1 fig.

—— 1983. Skelettfunde von *Kopidodon* (Condylarthra, Mammalia) aus dem mitteleozänen Ölschiefer von Messel bei Darmstadt. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **167** (1): 1–39, 23 figs, 2 tabs.

—— **& Schaarschmidt, F.** 1983. Ein Urpferd aus Messel, das Weinbeeren frass. *Natur Mus., Frankf.*, **113** (3): 79–84, 8 figs.

—— **& Storch, G.** 1983. *Pholidocercus hassiacus*, ein Amphilemuride aus dem Eozän der 'Grube Messel' bei Darmstadt (Mammalia, Lipotyphla). *Senckenberg. leth.*, Frankfurt a.M., **64** (5/6): 447–495, 27 figs, 3 tabs.

Korth, W. W. 1979. Taphonomy of microvertebrate fossil assemblages. *Ann. Carneg. Mus.*, Pittsburgh, **48** (15): 235–285.

Kowalevsky, W. 1874. Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Classification der fossilen Huftiere (2). *Palaeontographica*, Cassel, (NF) **2** (4): 211–290, pls 10–12.

Kretzoi, M. 1943. *Kochictis centennii* n.g. n.sp., az egeresi felső Oligocénből. *Földt. Közl.*, Budapest, **73:** 10–17, pl. 1. (Also in German: *Kochictis centennii* n.g. n.sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. *Loc. cit.*: 190–195).

Krutsch, W. & Lotsch, D. 1958. Übersicht über die paläogeographische Entwicklung des zentraleuropäischen Alttertiärs (ohne Tethys-Raum). *Ber. geol. Ges. D.D.R.*, Berlin, **3** (2/3): 99–110, pls 19–29.

—— —— 1964. Propositions à l'appui d'une tentative en vue de subdiviser les dépôts de l'Eocène supérieur et ceux de l'Oligocène inférieur et moyen et de mettre en parallèle ces dépôts d'Europe occidentale entre eux et avec ceux d'Europe centrale, et étude de la position à assigner à la limite entre l'Eocène et l'Oligocène dans ces régions. *Mém. Bur. Rech. géol. minièr.*, Paris, **28:** 949–963, 1 tab.

Kühne, W. G. 1969. A multituberculate from the Eocene of the London Basin. *Proc. geol. Soc.*, London, **1658:** 199–202, 1 fig.

Lapparent, A. de 1906. *Traité de Géologie*, 5th edn. 1288 pp., 583 figs. Paris.

Laurillard, C. L. 1849. Lophiodon. *In* d'Orbigny, A., *Dictionnaire Universel d'Histoire Naturelle*, **7:** 438–439. Paris.

Lavocat, R. 1951. *Révision de la faune des mammifères oligocènes d'Auvergne et du Velay.* 153 pp., 26 pls. Paris.

—— 1955. Sur un squelette de *Pseudosciurus* provenant du gisement d'Armissan (Aude). *Annls Paléont.*, Paris, **41:** 75–89, 11 figs, pl. 4.

Lawson, J. D. 1979. Stability of stratigraphic nomenclature. *Newsl. Stratigr.*, Leiden, 7 (3): 159–165.

Leach, W. E. 1814. *The Zoological Miscellany; being descriptions of new, or interesting animals*, **1.** 144 pp., 60 pls. London.

Leidy, J. 1856. Notices of the remains of extinct Mammalia discovered by Dr F. V. Hayden in Nebraska Territory. *Proc. Acad. nat. Sci. Philad.*, **8:** 88–90.

—— 1872. Remarks on fossils from Wyoming. *Proc. Acad. nat. Sci. Philad.*, **1872:** 277.

—— 1873. Contributions to the extinct vertebrate fauna of the Western Territories. *Rep. U.S. geol. Surv.*

Territ., Washington, (F. V. Hayden) **1** (1): 1–358, 37 pls.

Lemoine, M. (ed.) 1978. *Geological Atlas of Alpine Europe and Adjoining Alpine Areas.* 584 pp. Amsterdam, Oxford, New York.

Lemoine, P. & Abrard, R. 1926. Sur la présence de *Palaeotherium magnum* Cuvier dans le calcaire de Saint-Ouen. *Bull. Soc. géol. Fr.*, Paris, **26:** 3–9, 1 fig., pl. 1.

Lemoine, V. 1878. Communication sur les ossements fossiles des terrains tertiaires inférieures des environs de Reims faite à la Société d'Histoire Naturelle de Reims. *Bull. Soc. Hist. nat. Reims*, **2** (2): 90–113.

— 1880. Sur les ossements fossiles des terrains tertiaires inférieures des environs de Reims. *C.r. Ass. fr. Avanc. Sci.*, Paris, **8** (Montpellier 1879): 585–594.

— 1891. Étude d'ensemble sur les dents les mammifères fossiles des environs de Reims. *Bull. Soc. géol. Fr.*, Paris, (3) **19:** 253–290.

Lewis, G. E. 1933. Preliminary notice of a new genus of lemuroid from the Siwaliks. *Am. J. Sci.*, New Haven, (5) **26:** 134–138.

Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial–placental dichotomy in mammalian evolution. *Paleont. Contr. Univ. Kans.*, Lawrence, **50** (Vert. 12): 1–122, 53 figs, 21 tabs.

Linnaeus, C. 1758. *Systema Naturae* ... 10th edn, **1**. 824 pp. Stockholm.

Louis, P. 1976. Gisements de mammifères bartoniens du Tardenois. Remarques sur la paléogéographie de l'Auversien du sud de Fismes. *Bull. Inf. Géol. Bassin Paris*, **13** (2): 41–58, 3 figs, 2 tabs.

— **& Sudre, J.** 1975. Nouvelles données sur les Primates de l'Eocène supérieur européen. *Colloques int. Cent. natn. Rech. scient.*, Paris, Problèmes actuels de Paléontologie – Evolution des Vertébrés, no. **218:** 805–828, 5 figs, 2 pls.

Lydekker, R. 1883. Indian Tertiary and Post-Tertiary Vertebrata. Pt 5 – Siwalik selenodont Suina. *Mem. geol. Surv. India Palaeont. indica*, Calcutta, (10) **2** (5): 143–177, pls 23–25.

— 1887. *Catalogue of the Fossil Mammalia in the British Museum*, **5** (Group Tillodontia, Orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata and Supplement). xxxv + 345 pp., 55 figs. London.

Maack, G. A. 1865. *Palaeontologische Untersuchungen über noch unbekannte Lophiodonfossilien von Heidenheim am Hahnenkamme in Mittelfranken nebst einer kritischen Betrachtung sämmtlicher bis jetzt bekannten Species des Genus Lophiodon.* 76 pp., 14 pls. Leipzig.

Machin, J. 1971. Plant microfossils from the Tertiary deposits of the Isle of Wight. *New Phytol.*, London, Cambridge, **70:** 851–872.

MacIntyre, G. T. 1972. The trisulcate petrosal pattern of mammals. *Evol. Biol.*, New York, **6:** 275–303, 8 figs, 1 tab.

McKenna, M. C. 1962. Collecting small fossils by washing and screening. *Curator*, New York, **5** (3): 221–235, 6 figs.

— 1963. Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the Primate–Insectivore boundary. *Am. Mus. Novit.*, New York, **2160:** 1–39, 5 figs.

Maier, W. 1979. *Macrocranion tupaiodon*, an adapisoricid(?) insectivore from the Eocene of 'Grube Messel' (West Germany). *Paläont. Z.*, Stuttgart, **53** (1/2): 38–62, 8 figs, 1 tab.

Major, C. J. F. 1873. Nagerüberreste aus Bohnerzen Suddeutchlands und der Schweiz. *Palaeontographica*, Cassel, (NF) **2** (2): 75–130.

Marsh, O. C. 1871. Notice of some new fossil mammals and birds, from the Tertiary Formation of the West. *Am. J. Sci.*, New Haven, (3) **2:** 120–127.

— 1872. Preliminary description of new Tertiary mammals. *Am. J. Sci.*, New Haven, **4:** 122–128, 202–224.

Martini, E. 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation. *In* Farinacci, A. (ed.), *Proceedings of the II Planktonic Conference, Roma 1970*, **2:** 739–785, 4 pls. Rome.

Matthes, H. W. 1952. Die Creodontier aus der mitteleozänen Braunkohle des Geiseltales. *Hallesches Jb. mitteldt. Erdgesch.*, Halle, **1** (4): 201–240, pls 16–40, 4 figs.

— 1977. Die Equiden aus dem Eozän des Geiseltales. 1. Die Zähne. *In* Matthes, H. W. & Thaler, B., *Eozäne Wirbeltiere des Geiseltales*: 5–39, pls 1–159, 176. (**1**, text, 149 pp.; **2**, atlas, 176 pls). Halle, Martin-Luther Universität, Halle-Wittenberg.

Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin Middle Eocene. *Mem. Am. Mus. nat. Hist.*, New York, **9:** 289–567, pls 42–52, 118 figs.

— 1910. On the osteology and relationships of *Paramys* and the affinities of the Ischyromyidae. *Bull. Am. Mus. nat. Hist.*, New York, **28:** 43–71.

— 1928. The evolution of the mammals in the Eocene. *Proc. zool. Soc. Lond.*, **1927** (4): 947–985.

1929*a*. Critical observations upon Siwalik mammals. *Bull. Am. Mus. nat. Hist.*, New York, **56** (7): 437–560, figs 1–55.

—— 1929*b*. Reclassification of the Artiodactyl families. *Bull. geol. Soc. Am.*, New York, **40:** 403–408.

—— 1929*c*. Preoccupied names. *J. Mammal.*, Baltimore, **10** (2): 171.

—— **& Granger, W.** 1921. New genera of Paleocene mammals. *Am. Mus. Novit.*, New York, **13:** 1–7.

Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, London, **16:** 713–719.

Mayer [Eymar], K. 1857. Versuch einer neuen Klassifikation der Tertiär-Gebilde Europa's. *Verh. schweiz. naturf. Ges.*, Basel, **42:** 165–199.

—— 1869. *Tableau synchronistique des terrains Tertiaires inférieurs.* 4th edn, Zürich.

Mayhew, D. 1977. Avian predators as accumulators of fossil mammal material. *Boreas*, Oslo, **6:** 25–31, 3 figs.

Mein, P. & Freudenthal, M. 1971. Les Cricetidae (Mammalia, Rodentia) du Néogène Moyen de Vieux-Collonges. 1: Le genre *Cricetodon* Lartet, 1851. *Scr. geol.*, Leiden, **5:** 1–51, 6 pls, 13 figs.

Menu, H. & Sigé, B. 1971. Nyctalodontie et myotodontie, importants caractères de grades évolutifs chez les chiroptères entomophages. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **272:** 1735–1738, 1 pl.

Meyer, H. v. 1846. [Neue Säugthiere von Weisenau.] *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, **1846:** 473–475.

—— 1852. Mittheilungen an Professor Bronn gerichtet. *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, **1852:** 831–833.

Michaux, J. 1964. Diagnoses de quelques Paramyidés de l'Eocène inférieur de France. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1964:** 153.

—— 1968. Les Paramyidae (Rodentia) de l'Eocène inférieur du Bassin de Paris. *Palaeovertebrata*, Montpellier, **1** (4): 135–193, 10 pls, 4 figs, 2 tabs.

Miller, G.S. 1923. The telescoping of the cetacean skull. *Smithson. misc. Collns*, Washington, **76** (5): 1–72, pls 1–8.

—— **& Gidley, J. W.** 1918. Synopsis of the Supergeneric Groups of Rodents. *J. Wash. Acad. Sci.*, **8:** 431–448.

Misonne, X. 1957. Mammifères oligocènes de Hoogbutsel et Hoeleden; 1 – Rongeurs et ongulés. *Bull. Inst. r. Sci. nat. Belg.*, Brussels, **33** (51): 1–61.

Monty, C. L. V. & Hardie, L. 1976. The geological significance of the fresh water blue-green algal calcareous marsh. *In* Walter, M. R. (ed.), Stromatolites. *Devs Sedimentol.*, Amsterdam, **20:** 447–488.

Moody, R. T. J. 1980. Notes on some European Palaeogene Turtles. *Tert. Res.*, Rotterdam, **2** (4): 161–168, 1 fig., 1 tab.

Morellet, L. & Morellet, J. 1934. Que faut-il entendre par 'Bartonien' Mayer-Eymar 1857? *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1934** (5): 73–74.

—— —— 1948. Le Bartonien du Bassin de Paris. *Mém. Serv. Carte géol. dét. Fr.*, Paris. 437 pp.

Morlan, R. E. 1980. Taphonomy and archaeology in the upper Pleistocene of the northern Yukon Territory: a glimpse of the peopling of the New World. *Pap. archaeol. Surv. Can.*, Ottawa, (Mercury ser.) **94**. xxvii + 398 pp.

Morton, A. C. 1982. Heavy minerals of Hampshire Basin Palaeogene strata. *Geol. Mag.*, London, **119** (5): 463–476, 4 figs, 1 pl., 2 tabs.

Munier-Chalmas, E. & Lapparent, A. de 1893. Note sur la nomenclature des terrains sédimentaires. *Bull. Soc. géol. Fr.*, Paris, (3) **21:** 438–488.

Murray, J. W. & Wright, C. A. 1974. Palaeogene Foraminiferida and palaeocology, Hampshire and Paris Basins and the English Channel. *Spec. Pap. Palaeont.*, London, **14:** 1–129, 20 pls.

Muul, I. & Lim, B. L. 1978. Comparative morphology, food habits, and ecology of some Malaysian arboreal rodents. *In* Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*: 361–368, 7 figs, 6 tabs. Washington, D.C., Symp. natn. zool. Park, Smithson. Instn.

Myannil, R.M. 1966. O vertikalnykh norkakh zaryvaniya v Ordovikskikh izvestiyakakh Pribaltiki. *In* Gekker, P. F. (ed.), *Organizm i sreda v geologischeskom proshlom*: 200–207, figs 1–2, pls 1–2. Moskva, Leningrad (Nauka). (Not seen).

Nesbit Evans, E. M., Van Couvering, J. A. H. & Andrews, P. 1981. Palaeoecology of Miocene sites in western Kenya. *J. hum. Evol.*, London, **10:** 99–116, 11 figs, 1 tab.

Niemitz, C. 1977. Zur Funktionsmorphologie und Biometrie der Gattung *Tarsius* Storr, 1780 (Mammalia, Primates, Tarsiidae). *Cour. ForschInst. Senckenberg*, Frankfurt a.M., **25:** 1–161, 73 figs, 12 tabs.

Noulet, J.-B. 1851. Note sur une nouvelle espèce de *Lophiodon* (*Lophiodon lautricense*). *Mém. Acad. Sci. Inscript. Toulouse*, (4) **1:** 245–250.

—— 1863. Étude sur les fossiles du terrain Eocène supérieur du Bassin de l'Agout (Tarn). *Mém. Acad. Sci. Inscript. Toulouse*, (6) **1:** 181–206.

Novacek, M. J. 1976. Insectivora and Proteutheria of the later Eocene (Uintan) of San Diego County, California. *Contr. Sci. Los Angeles*, **283**. 53 pp., 19 figs, 6 tabs.

—— , **Bown, T. M. & Schankler, D.** 1985. On the classification of the early Tertiary Erinaceomorpha (Insectivora, Mammalia). *Am. Mus. Novit.*, New York, **2813:** 1–22, 11 figs, 1 tab.

Odin, G. S. & Curry, D. 1981. L'échelle numérique des temps paléogènes en 1981. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (2) **293** (14): 1003–1006.

—— —— **& Hunziker, J. C.** 1978. Radiometric dates from N.W. European glauconites and the Palaeogene time scale. *J. geol. Soc. Lond.*, **135:** 481–497, 2 figs, 4 tabs.

Ollivier-Pierre, M.-F. 1980. Étude palynologique (spores et pollens) de gisements paléogènes du Massif Armoricain. Stratigraphie et Paléogéographie. *Mém. Soc. géol. minér. Bretagne*, Rennes, **25:** 1–239, 33 pls, 29 figs.

Osborn, H. F. 1910. *The age of Mammals in Europe, Asia and North America*. xx + 635 pp., 220 figs. New York.

Owen, R. 1841. Description of some fossil remains of *Chaeropotamus*, *Palaeotherium*, *Anoplotherium* and *Dichobunes*, from the Eocene formation, Isle of Wight. *Trans. geol. Soc. Lond.*, (2) **6** (1): 41–45, pl. 4.

—— 1845. *Odontography; or a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure, in the vertebrate animals*, **3:** xli–lxxiv, 289–655; pls i, ii, 62A, 90–150. London.

—— 1846. *A History of British Fossil Mammals and Birds*. 560 pp., 236 figs. London.

—— 1848*a*. On the fossil remains of Mammalia referable to the genus Palaeotherium, and to two genera Paloplotherium and Dichodon, hitherto undefined, from the Eocene Sand at Hordle, Hampshire. *Q. Jl geol. Soc. Lond.*, **4:** 17–42, 6 figs, pls 3–4.

—— 1848*b*. Description of teeth and portions of jaws of two extinct Anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develope Cuvier's idea of the classification of pachyderms by the number of their toes. *Q. Jl geol. Soc. Lond.*, **4:** 103–141, pls 7–8, 13 figs.

—— 1857*a*. On the *Dichodon cuspidatus* Owen. *Q. Jl geol. Soc. Lond.*, **13:** 190–196, pl. 3.

—— 1857*b*. Description of the lower jaw and teeth of an Anoplotherioid quadruped (*Dichobune ovina*, Ow.) of the size of the *Xiphodon gracilis*, Cuv., from the Upper Eocene Marl, Isle of Wight. *Q. Jl geol. Soc. Lond.*, **13:** 254–260, pl. 8.

Palmer, C. P. 1975. Neogene structures in South-West England. *Tertiary Times*, Bromley, **2** (4): 178–184, 2 figs.

Parker, T. J. & Haswell, W. A. 1897. *A Text-book of Zoology*, **2**. xx + 683 pp. London.

Pavlow, M. 1900. Études sur l'histoire paléontologique des ongulés. 7. Artiodactyles anciens. *Bull. Soc. Nat. Moscou*, (n.s.) **13:** 266–328, 2 pls.

Pavoni, N. 1961. Faltung durch Horizontalverschiebung. *Eclog. geol. Helv.*, Lausanne, Basel, **54:** 515–534.

Pearson, H. S. 1927. On the skulls of early Tertiary Suidae, together with an account of the otic region in some other primitive Artiodactyla. *Phil. Trans. R. Soc.*, London, (B) **215:** 389–460, 53 figs.

Peterson, O. A. 1919. Report upon the material discovered in the upper Eocene of the Uinta basin by Earl Douglas in the years 1908–1909, and by O. A. Peterson in 1912. *Ann. Carneg. Mus.*, Pittsburgh, **12:** 40–168, pls 34–47.

Pictet, F.-J. 1857. Seconde Partie. Description des ossements fossiles trouvés au Mauremont. *In* Pictet, F.-J., Gaudin, C. & de la Harpe, P. 1855–57. *Mémoire sur les Animaux Vertébrés trouvés dans le terrain sidérolithique du canton de Vaud et appartenant à la faune éocène*: 27–120, pls 1–13. Geneva, Matériaux Paléont. Suisse (1) **2**.

—— **& Humbert, A.** 1869. *Mémoire sur les animaux vertébrés trouvés dans le terrain sidérolithique du Canton de Vaud et appartenant à la faune éocène. Supplément.* Geneva, Matériaux Paléont. Suisse, (5) **2:** 121–197, pls 14–28.

Pilgrim, G. E. 1941. The dispersal of the Artiodactyla. *Biol. Rev.*, Cambridge, **16:** 134–163.

Plaziat, J.-C. 1981. Late Cretaceous to late Eocene palaeogeographic evolution of southwest Europe. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **36:** 263–320, 24 figs, 1 tab.

Plint, A. G. 1982. Eocene sedimentation and tectonics in the Hampshire Basin. *J. geol. Soc. Lond.*, **139** (3): 249–254, 3 figs.

—— 1983. Sandy fluvial point-bar sediments from the Middle Eocene of Dorset, England. *Spec. Publs int. Ass. Sedimentol.*, Oxford, **6:** 355–368, 12 figs.

—— 1984. A regressive coastal sequence from the Upper Eocene of Hampshire, southern England. *Sedimentology*, Oxford, **31:** 213–225, 9 figs.

Pomel, A. 1847*a*. Note sur les mammifères et les reptiles fossiles des terrains éocènes de Paris, inférieurs au dépôt gypseux. *Archs Sci. phys. nat.*, Genève, **4:** 326–330.

—— 1847*b*. Note critique sur le genre *Palaeotherium*. *Bull. Soc. géol. Fr.*, Paris, (2) **4:** 584–587.

—— 1848. [Sur la classification des mammifères ongulés]. *Bull. Soc. géol. Fr.*, Paris (2) **5:** 256–257.

—— 1853. *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique superiur de la Loire et surtout dans la vallée de son affluent principal l'Allier*. 193 pp., Paris.

Pomerol, C. 1961. Corrélation entre le Lédien du Bassin de Bruxelles et le Lutétien supérieur du Bassin de Paris. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **253:** 3839–3841.

—— 1964. Le Bartonien du Bassin de Paris: Interprétation stratigraphique et essai de corrélation avec les bassins de Belgique et du Hampshire. *Mém. Bur. Rech. géol. minièr.*, Paris, **28:** 153–173.

—— 1967. Esquisse paléogéographique du Bassin de Paris à l'ère tertiaire et aux temps quaternaires. *Revue Géogr. phys. Géol. dyn.*, Paris, (2) **9** (1): 55–86, 17 figs.

—— 1973. *Stratigraphie et Paléogéographie. Ere Cénozoïque* (*Tertiaire et Quaternaire*). 269 pp., 235 figs. Paris.

—— 1980. Auversien. Marinésien. *In* Cavelier, C. & Roger, J., Les étages français et leurs stratotypes. *Mém. Bur. Rech. géol. minièr.*, Paris, **109:** 227–236.

Porrenga, D. H. 1967. Glauconite and chamosite as depth indicators in the marine environment. *Mar. Geol.*, Amsterdam, **5:** 495–501.

Pratt, S. P. 1835. Remarks on the Existence of the *Anoplotherium* and *Palaeotherium* in the Lower Freshwater Formation at Binstead, near Ryde, in the Isle of Wight. *Trans. geol. Soc. Lond.*, (2) **3** (3): 451–453, 2 figs.

Preece, R. 1976. A note on the terrestial Gastropoda of the Bembridge Limestone (Upper Eocene/Lower Oligocene) of the Isle of Wight, England. *Tert. Res.*, London, **1** (1): 17–19, 1 tab.

—— 1980*a*. The Mollusca of the Creechbarrow Limestone Formation (Eocene) of Creechbarrow Hill, Dorset. *Tert. Res.*, Rotterdam, **2** (4): 169–180, 4 pls, 2 figs.

—— 1980*b*. The biostratigraphy and dating of the tufa deposit at the Mesolithic site at Blashenwell, Dorset, England. *J. Archaeol. Sci.*, London, **7:** 345–362, 5 figs, 6 tabs.

—— 1981. The occurrence of *Proserpina* in the British Tertiary, with the description of a new species (Prosobranchia: Helicinidae). *Arch. Molluskenk.*, Frankfurt a.M., **111** (1/3): 49–54, 3 figs.

Prestwich, J. 1846. On the Tertiary or Supracretaceous Formations of the Isle of Wight as exhibited in the sections at Alum Bay and White Cliff Bay. *Q. Jl geol. Soc. Lond.*, **2:** 223–259.

—— 1847. On the probable age of the London Clay. *Q. Jl geol. Soc. Lond.*, **3:** 354–377.

—— 1849. On the position and general characters of the strata exhibited in the coast section from Christchurch Harbour to Poole Harbour. *Q. Jl geol. Soc. Lond.*, **5:** 43–49, 4 figs.

—— 1857. On the correlation of the Eocene Tertiaries of England, France and Belgium. Part 2 – the Paris Group. *Q. Jl geol. Soc. Lond.*, **13:** 89–134.

Quayle, W. J. 1982. A new Eocene isopod (Crustacea) from the Hampshire Basin. *Tert. Res.*, Rotterdam, **4** (1): 31–34, 1 pl.

—— **& Collins, J. S. H.** 1981. New Eocene crabs from the Hampshire Basin. *Palaeontology*, London, **24:** 733–758, pls 104–105, 2 figs.

Quinet, G. E. 1965. Un condylarthre de Hoogbutsel. *Bull. Inst. r. Sci. nat. Belg.*, Brussels, **41** (15): 1–5, 1 pl.

—— 1968. Les mammifères du Landénien continental belge; 2, étude de la morpholgie dentaire comparée des 'carnivores' de Dormaal. *Mém. Inst. r. Sci. nat. Belg.*, Brussels, **158:** 1–64, 7 pls, 4 figs.

Radinsky, L. 1964. *Paleomoropus*, a new early Eocene Chalicothere (Mammalia, Perissodactyla), and a revision of Eocene Chalicotheres. *Am. Mus. Novit.*, New York, **2179:** 1–28, 3 figs.

Rasmussen, H. W. 1972. Lower Tertiary Crinoidea, Asteroidea and Ophiuroidea from northern Europe and Greenland. *Biol. Skr.*, Copenhagen, **19** (7): 1–83, 14 pls, 5 figs.

Ratcliffe, B. C. & Fagerstrom, J. A. 1980. Invertebrate Lebensspuren of Holocene floodplains: their morphology, origin and palaeoecological significance. *J. Paleont.*, Chicago, **54** (3): 614–630, 1 pl., 4 figs.

Read, J. F. 1976. Calcretes and their distinction from stromatolites. *In* Walter, M. R. (ed.), Stromatolites. *Dev. Sedimentol.*, Amsterdam, **20:** 55–71, 3 pls.

Reid, C. 1898. The geology of the country around Bournemouth. *Mem. geol. Surv. U.K.*, London, sheet **329**. iv + 72 pp.

—— 1902*a*. The geology of the country around Ringwood. *Mem. geol. Surv. U.K.*, London, sheet **314**. iv + 62 pp., 4 figs.

—— 1902*b*. The geology of the country around Southampton. *Mem. geol. Surv. U.K.*, London, sheet **315**. iv + 70 pp., 21 figs.

Reineck, H.-E. & Singh, I. B. 1980. *Depositional sedimentary environments, with reference to terrigenous clastics*. 2nd edn. 549 pp., 683 figs. Berlin, Heidelberg, New York.

Remy, J.-A. 1965. Un nouveau genre de Paléothéridé (Perissodactyla) de l'Eocène supérieur du Midi de la France. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **260:** 4362–4364, 1 fig.

—— 1967. Les Palaeotheridae (Perissodactyla) de la faune de mammifères de Fons 1 (Eocène supérieur). *Palaeovertebrata*, Montpellier, **1** (1): 1–46, 20 figs, 8 pls, 12 tabs.

—— 1972. Étude du crâne de *Pachynolophus lavocati* n. sp. (Perissodactyla, Palaeotheriidae) des Phosphorites du Quercy. *Palaeovertebrata*, Montpellier, **5** (2): 45–78, 14 figs, 5 pls, 3 tabs.

—— 1976. *Étude comparative des structures dentaires chez les Palaeotheriidae et divers autres perissodactyles fossiles* (Thèse presentée pour le doctorat de 3ème cycle en sciences odontologiques, Faculté de chirurgie dentaire, Université Louis Pasteur). 207 pp, 32 figs, 14 pls, 39 tabs. Strasbourg.

Revilliod, P. 1917*a*. Fledermäuse aus der Braunkohle von Messel bei Darmstadt. *Abh. hess. geol. Landesanst.*, Darmstadt, **7** (2): 161–201, 1 pl., 18 figs, 4 tabs.

—— 1917*b*. Contribution à l'étude des chiroptères des terrains tertiaires. Part 1. *Abh. schweiz. paläont. Ges.*, Basel, **42:** 1–57, 13 figs, 1 pl.

Rich, T. H. U. 1971. Deltatheridia, Carnivora, and Condylarthra (Mammalia) of the early Eocene, Paris Basin, France. *Univ. Calif. Publs geol. Sci.*, Berkeley, **88:** 1–72, 18 figs, 32 tabs.

Richard, M. 1946. Contribution à l'étude du bassin d'Aquitaine. Les gisements de mammifères tertiaires. *Mém. Soc. géol. Fr.*, Paris, (NS) **24** (52): 1–380, 52 figs.

Richter, G. 1981. Untersuchungen zur Ernährung von *Messelobunodon schaeferi* (Mammalia, Artiodactyla). *Senckenberg. leth.*, Frankfurt, a.M., **61** (3/6): 355–370, 12 figs.

Ride, W. D. L. 1964. A review of the Australian fossil Marsupials. *J. Proc. R. Soc. West. Aust.*, Perth, **47** (4): 97–131, 13 figs, 3 tabs.

Robinson, P. 1968. Nyctitheriidae (Mammalia, Insectivora) from the Bridger Formation of Wyoming. *Contr. Geol. Univ. Wyo.*, Laramie, **7** (2): 129–138, pls 1–2.

Roman, F. 1904. Contributions à l'étude des bassins lacustres de l'Eocène et de l'Oligocène du Languedoc. *Bull. Soc. géol. Fr.*, Paris, (4) **3** (5): 546–616, 22 figs, pls 19–20.

Romer, A. S. 1966. *Vertebrate Paleontology*. ix + 468 pp. Chicago and London.

Russell, D. E. 1964. Les mammifères paléocènes d'Europe. *Mém. Mus. natn. Hist. nat., Paris*, **13** (C, Sci. terre): 1–321, 16 pls, 73 figs.

——**, Godinot, M., Louis, P. & Savage, D. E.** 1979. Apatotheria (Mammalia) de l'Eocène inférieur de France et de Belgique. *Bull. Mus. Hist. nat., Paris*, (4) **1** (C) (3): 203–243, 4 figs, 5 pls, 2 tabs.

——**, Louis, P. & Savage, D. E.** 1967. Primates of the French early Eocene. *Univ. Calif. publs geol. Sci.*, Berkeley, **73**. vi + 46 pp., 14 figs.

—— —— —— 1973. Chiroptera and Dermoptera of the French early Eocene. *Univ. Calif. Publs geol. Sci.*, Berkeley, **95:** 1–57, 13 figs.

—— —— —— 1975. Les Adapisoricidae de l'Eocène Inférieur de France. Réévaluation des formes considérées affines. *Bull. Mus. natn. Hist. nat. Paris*, (3) **45** (Sci. terre) (327): 129–193, 7 pls.

—— **& McKenna, M. C.** 1962. Étude de *Paroxyclaenus*, mammifère des Phosphorites du Quercy. *Bull. Soc. géol. Fr.*, Paris, (7) **3:** 274–282, 1 fig.

—— **& Sigé, B.** 1970. Révision des chiroptères Lutétiens de Messel (Hesse, Allemagne). *Palaeovertebrata*, Montpellier, **3** (4): 83–182, 29 figs, 6 pls, 5 tabs.

—— ***et al.*** 1982. Tetrapods of the Northwest European Tertiary Basin. *Geol. Jb.*, Hannover, (A) **60:** 1–74.

Rütimeyer, L. 1862. Eocaene Säugethiere aus dem Gebiet des schweizerischen Jura. *Neue Denkschr. Allg. schweiz. Ges. ges. Naturw.*, Zürich, **19:** 1–98.

—— 1888. Über einige Beziehungen zwischen den Säugethierstämmen alter und neuer Welt. Erster Nachtrag zu der eocänen Fauna von Egerkingen. *Abh. schweiz. paläont. Ges.*, Basel, **15:** 1–63, 1 pl.

—— 1890. Übersicht der eocänen Fauna von Egerkingen nebst einer Erwiederung an Prof. E. D. Cope. Zweiter Nachtrag zu der Eocänen Fauna von Egerkingen (1862). *Abh. schweiz. paläont. Ges.*, Basel, **17:** 1–24.

—— 1891. Die Eocäne Säugethier-Welt von Egerkingen. Gesammtdarstellung und dritten Nachtrag zu den 'Eocänen Säugethieren aus dem Gebiet des schweizerischen Jura' (1862). *Abh. schweiz. paläont. Ges.*, Basel, **18:** 1–153, 8 pls. [N.B. Plates apparently published in 1892].

Saban, R. 1954. Phylogénie des insectivores. *Bull. Mus. Hist. nat. Paris*, (2) **26:** 419–432.

Savage, D. E. & Russell, D. E. 1977. Comments on mammalian paleontologic stratigraphy and geochronology; Eocene stages and mammal ages of Europe and North America. *Géobios*, Lyon, (Mém. spec.) **1:** 47–56, 2 figs.

—— —— **& Louis, P.** 1965. European Eocene Equidae (Perissodactyla). *Univ. Calif. publs geol. Sci.*, Berkeley, **56**. v + 94 pp., 42 figs, 1 pl.

—— —— —— 1966. Ceratomorpha and Ancylopoda (Perissodactyla) from the Lower Eocene Paris Basin, France. *Univ. Calif. publs geol. Sci.*, Berkeley, **66**. v + 38 pp., 28 figs.

Schaub, S. 1958. Simplicidentata (Rodentia). *In* Piveteau, J., *Traité de Paléontologie* **6** (2): 659–818. Paris.

Schlosser, M. 1884. Die Nager des europäischen Tertiärs. *Palaeontographica*, Cassel, **31** (3): 1–143 (19–

161), pls 1–8 (5–12).

—— 1886. Beiträge zur Kentniss der Stammesgeschichte der Huftiere und Versuch einer Systematik der Paar- und Unpaarhufer. *Morph. Jb.*, Leipzig, **12:** 1–136, 6 pls.

—— 1887–90. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europäischen Tertiärs. 1. *Beitr. Paläont. Geol. Öst.-Ung.*, Wien, Leipzig, **6:** 1–224, pls 1–5 (1887). 3. *Loc. cit.* **8** (1, 2): 1–106, 2 tabs (1890).

Schmid, P. 1979. Evidence of Microchoerine Evolution from Dielsdorf (Zürich Region, Switzerland) – a Preliminary Report. *Folia primatol.*, Basel, **31:** 301–311, 5 figs, 2 tabs.

Schmidt-Kittler, N. 1970. Ein neue Pseudosciuride von Ehrenstein westlich Ulm. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **10:** 433–440.

—— 1971*a*. Odontologische Untersuchungen an Pseudosciuriden (Rodentia, Mammalia) des Alttertiärs. *Abh. bayer. Akad. Wiss.*, Munich, Math.-naturw. Kl., (NF) **150:** 1–133, 2 pls, 46 figs, 8 tabs.

—— 1971*b*. Eine unteroligozäne Primatenfauna von Ehrenstein bei Ulm. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **11:** 171–204, 33 figs, 5 tabs, pl. 13.

—— 1977*a*. Neue Primatenfunde aus unteroligozänen Karstspaltenfüllungen Süddeutschlands. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **17:** 177–195.

—— 1977*b*. Some aspects of evolution and provincialism of rodent faunas in the European Paleogene. *Géobios*, Lyon, (Mém. spéc.) **1:** 97–106, 3 figs.

—— **& Vianey-Liaud, M.** 1975. Les relations entre les faunes de rongeurs d'Allemagne du Sud de France pendant l'Oligocène. *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **281** (9): 511–514, pl. 1.

Schroeder, H. 1916. Eozäne Säugetierreste aus Nord- und Mitteldeutschland. *Jb. preuss. geol. Landesanst. BergAkad.*, Berlin, **37:** 164–195.

Schwartz, J. H. & Krishtalka, L. 1976. The lower antemolar teeth of *Litolestes ignotus*, a late Paleocene erinaceid (Mammalia, Insectivora). *Ann. Carneg. Mus.*, Pittsburgh, **46** (1): 1–6, 4 figs.

—— **& Tattersall, I.** 1985. Evolutionary relationships of living lemurs and lorises (Mammalia, Primates) and their potential affinities with European Eocene Adapidae. *Anthrop. Pap. Am. Mus. nat. Hist.*, New York, **60** (1): 1–100, 40 figs.

Scott, W. B. & Jepsen, G. L. 1936. The mammalian fauna of the White River Oligocene – Part 1. Insectivora and Carnivora. *Trans. Am. phil. Soc.*, Philadelphia, (NS) **28** (1): 1–153, 7 figs, 22 pls.

—— **& Osborn, H. F.** 1890. The Mammalia of the Uinta Formation. *Trans. Am. phil. Soc.*, Philadelphia, **16:** 461–572.

Seeley, H. G. 1876. Notice of the occurrence of remains of a British fossil Zeuglodon (*Z. Wanklyni* Seeley) in the Barton Clay of the Hampshire Coast. *Q. Jl geol. Soc. Lond.*, **32:** 428–432.

Seligsohn, D. & Szalay, F. S. 1978. Relationship between natural selection and dental morphology: tooth function and diet in *Lepilemur* and *Hapalemur*. *In* Butler, P. M. & Joysey, K. A., *Development, Function and Evolution of Teeth*: 289–307, 6 figs. London, New York, San Francisco.

Shearman, D. J. 1968. On Tertiary fault movements in North Devonshire. *Proc. Geol. Ass.*, London, **78** (4): 555–566, 3 figs, pls 16–17.

Shelubsky, M. 1951. Observations on the properties of a toxin produced by *Microcystis*. *Verh. int. Verein. theor. angew. Limnol.*, Stuttgart, **11:** 362–366, 3 tabs.

Sigé, B. 1975. Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale. Apatemyidés et Leptictidés. *Colloques Int. Cent. natn. Rech. scient.*, Paris. Problèmes actuels de Paléontologie – Evolution des Vertébrés, no. **218:** 653–672, 9 figs, 2 pls, 2 tabs.

—— 1976. Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale. Nyctithériidés. *Mém. Mus. natn. Hist. nat., Paris*, (C, Sci. terre) **34:** 1–140, 111 figs, 36 tabs.

—— 1978. 8, Insectivores et chiroptères. *In* La poche à phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. *Palaeovertebrata*, Montpellier, **8** (2–4): 243–268, 2 figs, 2 pls, 5 tabs.

Simons, E. L. 1961. Notes on some Eocene tarsioids and a revision of some Necrolemurinae. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **5:** 45–69, pls 12–14.

—— 1962. A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **7:** 1–36, 3 pls, 4 figs.

—— 1963. A critical reappraisal of Tertiary primates. *In* Buettner-Janusch (ed.), *Evolutionary and genetic biology of primates*, **1:** 65–129. New York & London.

Simpson, G. G. 1927. Mesozoic Mammalia VIII – Genera of Lance mammals other than multituberculates. *Am. J. Sci.*, New Haven, (5) **14** (80): 121–130.

—— 1928. A new mammalian fauna from the Fort Union of southern Montåna. *Am. Mus. Novit.*, New York, **297:** 1–15.

—— 1931. A new classification of mammals. *Bull. Am. Mus. nat. Hist.*, New York, **59:** 259–293.

—— 1940. Studies on the earliest primates. *Bull. Am. Mus. nat. Hist.*, New York, **77:** 185–212, 8 figs.

—— 1941. A giant rodent from the Oligocene of South Dakota. *Am. Mus. Novit.*, New York, **1149:** 1–16.

—— 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.*, New York, **85**. xvi + 350 pp.

——, **Roe, A. & Lewontin, R. C.** 1960. *Quantitative Zoology*, revised edn. 440 pp., 64 figs, 16 + v tabs. New York.

Sisson, S. & Grossman, J. D. 1953. *The Anatomy of the Domestic Animals*, 4th edn, rev. 972 pp., 738 figs. Philadelphia & London.

Sittler, C. 1969. L'Eocène dans le Fossé rhénan. *In* Colloque sur l'Eocène, Paris, Mai 1968, **3**. *Mém. Bur. Rech. géol. minièr., Paris*, **69:** 371–383, 1 tab.

Small, R. J. 1980. The Tertiary geomorphological evolution of south-east England: an alternative interpretation. *In* Jones, D. K. C., *The Shaping of Southern England*: 49–70, 6 figs. London, &c.; Inst. Br. Geogrs spec. Publ. **11**.

Smith, J. D., Richter, G. & Storch, G. 1979. Wie Fledermäuse sich einmal ernährt haben. *Umschau*, Frankfurt a.M. and Leipzig, **79** (15): 282–284.

Springhorn, R. 1980. *Paroodectes feisti*, der erste Miacide (Carnivora, Mammalia) aus dem Mittel-Eozän von Messel. *Paläont. Z.*, Berlin, **54** (1/2): 171–198, 10 figs, 2 tabs.

—— 1982. Neue Raubtiere (Mammalia: Creodonta et Carnivora) aus dem Lutetium der Grube Messel (Deutschland). *Palaeontographica*, Stuttgart, (A) **179:** 105–141, 15 pls, 9 text-figs, 5 tabs.

Stamp, L. D. 1921. On cycles of sedimentation in the Eocene strata of the Anglo–Franco–Belgian basin. *Geol. Mag.*, London, **58:** 146–157.

Stehlin, H. G. 1903–16. Die Säugetiere des schweizerischen Eocaens. Critischer Catalog der Materialen. 1. Die Fundorte, die Sammlungen – *Chasmotherium – Lophiodon. Abh. schweiz. paläont. Ges.*, Basel, **30:** i–vi, 1–153, figs 1–5, pls 1–3 (1903). 2. *Palaeotherium – Plagiolophus – Propalaeotherium. Loc. cit.* **31:** 155–258, figs 6–13, pls 4–7 (1904*b*). 2 (cont.). *Palaeotherium – Plagiolophus – Propalaeotherium. Loc. cit.* **32:** 259–445, figs 14–30, pls 8–9 (1905*a*). 3. *Lophiotherium – Anchilophus – Pachynolophus.* Nachträge – Schlussbetrachtungen über die Perissodactylen. *Loc. cit.* **32:** 447–595, figs 31–64, pls 10–11 (1905*b*). 4. *Dichobune – Mouillacitherium – Meniscodon – Oxacron. Loc. cit.* **33:** 597–690, figs 65–98, pl. 12 (1906). 5. *Choeropotamus – Cebochoerus – Choeromorus – Haplobunodon – Rhagatherium – Mixtotherium. Loc. cit.* **35:** 691–837, figs 99–133, pls 13–14 (1908). 6. *Catodontherium – Dacrytherium – Leptotheridium – Anoplotherium – Diplobune – Xiphodon – Pseudamphimeryx – Amphimeryx – Dichodon – Haplomeryx – Tapirulus – Gelocus* – Nachträge – Artiodactyla incertae sedis – Schlussbetrachtungen über die Artiodactylen – Nachträge zu den Perissodactylen. *Loc. cit.* **36:** 839–1164, figs 134–243, pls 15–20 (1910*b*). 7(1). *Adapis. Loc. cit.* **38:** 1165–1298, figs 244–289 (1912). 7(2). *Caenopithecus – Necrolemur – Microchoerus – Nannopithex – Anchomomys – Periconodon – Amphichiromys – Heterochiromys* – Nachträge zu *Adapis* – Schlussbetrachtungen zu den Primaten. *Loc. cit.* **41:** 1299–1552, figs 290–371, pls 21–22 (1916).

—— 1904*a*. Sur les mammifères des sables bartoniens du Castrais. *Bull. Soc. géol. Fr.*, Paris, (4) **4:** 445–475, 2 figs, pls 11–12.

—— 1904*b*–08. See 1903–16.

—— 1910*a*. Remarques sur les faunules de Mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bull. Soc. géol. Fr.*, Paris, (4) **9:** 488–520.

—— 1910*b*–16. See 1903–16.

—— 1918. Le *Pernatherium rugosum* P. Gervais. *Bull. Soc. géol. Fr.*, Paris, (4) **18:** 123–138.

—— 1940. Zur Stammesgeschichte der Soriciden. *Eclog. geol. Helv.*, Lausanne, Basel, **33:** 298–306, 5 figs.

—— **& Schaub, S.** 1951. Die Trigonodontie der simplicidentaten Nager. *Abh. schweiz. paläont. Ges.*, Basel, **67:** 1–385.

Stinton, F. C. 1970. Field Meeting in the New Forest, Hants. *Proc. Geol. Ass.*, London, **81:** 269–274.

—— 1975–80. Fish otoliths from the English Eocene. 258 pp., 16 pls. *Palaeontogr. Soc. (Monogr.)*, London.

—— **& Curry, D.** 1979. Lithostratigraphical nomenclature of the English Palaeogene succession. *Geol. Mag.*, London, **116:** 66–67.

Stock, C. 1934. New Creodonta from the Sespe upper Eocene, California. *Proc. natn. Acad. Sci. U.S.A.*, Washington, **20:** 423–427, 1 pl.

Storch, G. 1978. *Eomanis waldi*, ein Schuppentier aus dem Mittel-Eozän der 'Grube Messel' bei Darmstadt (Mammalia, Pholidota). *Senckenberg. leth.*, Frankfurt, a.M., **59** (4/6): 503–529, 5 pls, 5 figs.

—— 1981. *Eurotamandua joresi* ein Myrmecophagide aus dem Eozän der 'Grube Messel' bei Darmstadt (Mammalia, Xenarthra). *Senckenberg. leth.*, Frankfurt, a.M., **61** (3/6): 247–289, 14 figs, 3 pls.

Sturm, M. 1978. Maw contents of an Eocene Horse (*Propalaeotherium*) out of the oil shale of Messel near Darmstadt. *In* Kvacek, Z. & Schaarschmidt, F. (eds), International Symposium Advances in Angiosperm Palaeobotany, Liblice (ČSSR), June 13–17, 1977. *Cour. ForschInst. Senckenberg*, Frankfurt a.M., **30**: 120–122.

Sudre, J. 1969*a*. Les gisements de Robiac (Eocène supérieur) et leurs faunes de mammifères. *Palaeovertebrata*, Montpellier, **2**: 95–156, 21 figs.

—— 1969*b*. Acquisitions récentes pour la faune des Mammifères de Robiac. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1969** (4): 125–126, 1 fig.

—— 1971. Étude de variabilité chez *Lophiodon lautricense* Noulet. *Palaeovertebrata*, Montpellier, **4** (3): 67–95, 11 figs, 4 pls, 5 tabs.

—— 1972. Révision des artiodactyles de l'Eocène moyen de Lissieu (Rhône). *Palaeovertebrata*, Montpellier, **5** (4): 111–156, 17 figs, 7 tabs.

—— 1973. Un *Dichodon* géant de La Débruge et une nouvelle interprétation phylétique du genre. *Bull. Mus. natn. Hist. nat. Paris*, (3) **25** (Sci. terre) (133): 73–78, 1 fig. 1 tab.

—— 1974. L'endémisme des faunes de mammifères du Sud de l'Angleterre à l'Eocène supérieur. *Réun. a. Sci. Terre*, Paris, **2**: 362.

—— 1978*a*. 9. Primates et Artiodactyles. *In* La Poche à phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. *Palaeovertebrata*, Montpellier, **8** (2–4): 269–290, 5 figs, 6 tabs.

—— 1978*b*. Les artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale (systématique et évolution). *Mém. Trav. Inst. Montpellier*, **7**: 1–229, 23 figs, 33 pls.

—— 1980. *Aumelasia gabineaudi* n.g. n.sp., nouveau Dichobunidae (Artiodactyla, Mammalia) du gisement d'Aumelas (Hérault) d'age Lutétien terminal. *Palaeovertebrata*, Montpellier, **Mém. jub. Lavocat**: 197–211, 3 figs, 2 tabs.

Swindler, D. R. 1976. *Dentition of Living Primates*. xvii + 308 pp., 55 figs, 214 tabs. London, New York & San Francisco.

Szalay, F. S. 1968. Origins of the Apatemyidae (Mammalia, Insectivora). *Am. Mus. Novit.*, New York, **2352**: 1–11, 4 figs, 1 tab.

—— 1969. Mixodectidae, Microsyopidae, and the insectivore–primate transition. *Bull. Am. Mus. nat. Hist.*, New York, **140** (4): 163–330, pls 17–57, 28 figs, 21 tabs.

—— 1971*a*. The European Adapid Primates *Agerina* and *Pronycticebus*. *Am. Mus. Novit.*, New York, **2466**: 1–19, 13 figs, 1 tab.

—— 1971*b*. Relationships of the alleged primate *Gesneropithex peyeri* Hürzeler, 1946. *J. Mammal.*, Baltimore, **52** (4): 824–826, 1 fig.

—— 1974. New genera of European Adapid Primates. *Folia Primatol.*, Basel, **22** (2–3): 116–133, 10 figs.

—— 1975. Phylogeny, adaptation and dispersal of the tarsiiform primates. *In* Luckett, W. P. & Szalay, F. S. (eds), *Phylogeny of the Primates: A Multidisciplinary Approach*: 357–404, 19 figs. New York.

—— 1976. Systematics of the Omomyidae (Tarsiiformes, Primates); taxonomy, phylogeny and adaptations. *Bull. Am. Mus. nat. Hist.*, New York, **156** (3): 157–450, 178 figs, 29 tabs.

—— **& Delson, E.** 1979. *Evolutionary History of the Primates*. xiv + 580 pp., 263 figs. New York, &c.

Tattersall, I. & Schwartz, J. H. 1984. A new genus and species of adapid primate from the middle Eocene of Alsace, and a new genus for *'Adapis' ruetimeyeri* Stehlin 1912. *Folia Primatol.*, Basel, **41** (3–4): 231–239.

Tawney, E. B. 1882. On the Upper Bagshot Sands of Hordwell Cliffs, Hampshire. *Proc. Camb. phil. Soc. math. phys. Sci.*, **4**: 140–155.

Teilhard de Chardin, P. 1915. Les carnassiers des Phosphorites du Quercy. *Annls Paléont.*, Paris, **9** (3–4): 101–191, pls 12–20, 13 figs, 8 tabs.

—— 1921. Sur quelques primates des Phosphorites du Quercy. *Annls Paléont.*, Paris, **10**: 1–20, 6 figs, pls 1–2.

—— 1922. Les mammifères de l'Eocène inférieur français et leurs gisements. *Annls Paléont.*, Paris, **11**: 1–116, 42 figs, pls 1–8.

—— 1927. Les mammifères de l'Eocène inférieur de la Belgique. *Mém. Mus. r. Hist. nat. Belg.*, Brussels, **36**: 1–33, 29 figs, 6 pls, 1 tab.

Thaler, L. 1965. Une échelle de zones biochronologiques pour les mammifères du Tertiaire d'Europe. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1965**: 118.

—— 1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. *Mém. Mus. natn. Hist. nat. Paris*, (C, Sci. terre) **17**: 1–296, 25 figs, 27 pls, 13 tabs.

—— 1972. Datation, zonation et mammifères. *Mém. Bur. Rech. géol. minièr.*, Paris, **77**: 411–424, 4 tabs.

Thomas, H. 1906. Note sur un gisement de *Lophiodon* à Sergy, au Sud-Est de Fère-en-Tardenois (Aisne). *Bull. Soc. géol. Fr.*, Paris, (4) **6**: 686–688.

Tobien, H. 1961. Ein *Lophiodon*-Fund (Tapiroidea, Mamm.) aus den niederhessischen Braunkohlen. *Notizbl. hess. Landesamt. Bodenforsch. Wiesbaden*, **89:** 7–16, 1 fig., 1 pl.

—— 1969. *Kopidodon* (Condylarthra, Mammalia) aus dem Mitteleozän (Lutetium) von Messel bei Darmstadt (Hessen). *Notizbl. hess. Landesamt. Bodenforsch. Wiesbaden*, **97:** 7–37, pls 1–3, 7 figs, 9 tabs.

—— 1980. Ein anthracotherioider Paarhufer (Artiodactyla, Mammalia) aus dem Eozän von Messel bei Darmstadt (Hessen). *Geol. Jb. Hessen*, **108:** 11–22, 1 fig., 2 pls.

Trouessart, E. L. 1879. Catalogue des mammifères vivants et fossiles. Insectivores. *Revue Mag. Zool.*, Paris, (3) **7:** 219–285.

—— 1885. Catalogue des mammifères vivants et fossiles (Carnivores). *Bull. Soc. Etud. scient. Angers*, **1884** (Suppl.): 1–108.

True, F. W. 1908. The fossil cetacean *Dorudon serratus* Gibbes. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **52** (4): 65–78, 2 figs, 3 pls.

Tullberg, T. 1899. Über das System der Nagethiere, eine phylogenetische Studie. I-II. *Nova Acta R. Soc. Scient. upsal.*, (3) **18** (1) (sect. 2): 1–328.

Vail, P. R. & Hardenbol, J. 1979. Sea-level changes during the Tertiary. *Oceanus*, Woods Hole, Mass., **22** (3): 71–79, 11 figs.

Van Valen, L. 1964. Nature of the supernumerary molars of *Otocyon*. *J. Mammal.*, Baltimore, **45** (2): 284–286.

—— 1965. Paroxyclaenidae, an extinct family of Eurasian mammals. *J. Mammal.*, Baltimore, **46** (3): 388–397, 4 figs, 1 tab.

—— 1966. Deltatheridia, a new order of mammals. *Bull. Am. Mus. nat. Hist.*, New York, **132:** 1–126, pls 1–8, 17 figs.

—— 1967. New Paleocene insectivores and insectivore classification. *Bull. Am. Mus. nat. Hist.*, New York, **135** (5): 217–284, pls 6–7, 7 figs, 7 tabs.

—— 1978. The beginning of the Age of Mammals. *Evol. Theory*, Chicago, **4:** 45–80, 4 pls, 7 figs.

Vialov, O. S. & Sukatsheva, I. D. 1976. [Fossil caddisfly cases (Insecta, Trichoptera) and their stratigraphical value.] *In* Kramarenko, N. N., Paleontologiya i Biostratigrafiya Mongolii. *Trudȳ sovmest. sov.-mongol'. paleont. Eksped.*, Moscow, **3:** 169–232, 7 figs, 9 pls. [In Russian].

Vianey-Liaud, M. 1979. Evolution des rongeurs à l'Oligocène en Europe occidentale. *Palaeontographica*, Stuttgart, (A) **166:** 136–236, 64 figs, 17 tabs.

Viret, J. 1958–61. Perissodactyla. *In* Piveteau, J., *Traité de Paléontologie* **6** (2): 368–475, 112 figs (1958). Artiodactyla. *Loc. cit.* **6** (1): 887–1084, 166 figs (1961). Paris.

Wahlert, J. H. 1974. The cranial Foramina of Protrogomorphous Rodents; An Anatomical and Phylogenetic Study. *Bull. Mus. comp. Zool. Harvard*, Cambridge, Mass., **146** (8): 363–410, 13 figs.

Walker, C. A. 1980. The distribution of birds in the English Palaeogene. *In* Hooker *et al.* 1980. *Tert. Res.*, Rotterdam, **3** (1): 25–30.

Walker, E. P. 1975. *Mammals of the World*, 3rd edn. 1500 pp. Baltimore, London.

Ward, D. J. 1980. The distribution of sharks, rays and chimaeroids in the English Palaeogene. *In* Hooker *et al.* 1980. *Tert. Res.*, Rotterdam, **3** (1): 13–19.

Watelet, A. 1864. [Sur des Lophiodons découverts à Jouy (Aisne)]. *Bull. Soc. géol. Fr.*, Paris, (2) **21:** 298–300.

Weigelt, J. 1933. Neue Primaten aus den mitteleozänen (oberlutetischen) Braunkohle des Geiseltals (geborgen 1932 in der Gruben Cecilie und Leonhardt). *Nova Acta Leopoldina*, Halle a.S., (NF) **1:** 97–156, 11 pls, 3 figs.

Weitzel, K. 1933. *Kopidodon macrognathus* Wittich, ein Raubtier aus dem Mitteleozän von Messel. *Notizbl. Ver. Erdk. Darmstadt*, (5) **14:** 81–88, pl. 7.

—— 1949. Neue Wirbeltiere (Rodentia, Insectivora, Testudinata) aus dem Mitteleozän von Messel-bei-Darmstadt. *Abh. senckenb. Naturforsch. Ges.*, Frankfurt a.M., **480:** 1–24, 5 pls.

West, R. M. 1973. Review of the North American Eocene and Oligocene Apatemyidae (Mammalia, Insectivora). *Spec. Publs Mus. Tex. Tech. Univ.*, Lubbock, **3**. 42 pp., 20 figs, 8 tabs.

—— 1974. New North American Middle Eocene Nyctithere (Mammalia, Insectivora). *J. Paleont.*, Tulsa, **48** (5): 983–987, 1 pl.

Western, D. 1980. Linking the ecology of past and present mammal communities. *In* Behrensmeyer, A. K. & Hill, A. P. (eds), *Fossils in the Making. Vertebrate Taphonomy and Paleoecology*: 41–54, 6 figs. Chicago, London.

Whitaker, W. 1910. The water supply of Hampshire (including the Isle of Wight), with records of sinkings and borings. *Mem. geol. Surv. U.K.*, London. vi + 252 pp., 1 pl.

—— 1917. Some Hampshire wells. *Pap. Proc. Hamps. Fld Club*, Southampton, **8:** 40–64.

White, H. J. O. 1915. The geology of the country near Lymington and Portsmouth. Explanations of sheets

330 and 331 (mainland). *Mem. geol. Surv. U.K.*, London. v + 78 pp., 15 figs.

—— 1921*a*. A short account of the geology of the Isle of Wight. *Mem. geol. Surv. U.K.*, London. v + 219 pp.

—— 1921*b*. Appendix II. Report on sections exposed in excavations for sewers in the parish of Brockenhurst, Hants. *Mem. geol. Surv. Summ. Prog.*, London, **1920:** 81–84.

Wilson, J. A. & Szalay, F. S. 1976. New adapid primate of European affinities from Texas. *Folia Primatol.*, Basel, **25:** 294–312.

—— —— 1977. *Mahgarita*, new name for *Margarita* Wilson & Szalay, 1976, *non* Leach 1814 (1819, Lea, 1836, 1838, Lister, 1894). *J. Paleont.*, Tulsa, **51:** 643.

Wolfe, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Am. Scient.*, New Haven, **66:** 694–703.

—— 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern Hemisphere and Australasia. *Prof. Pap. U.S. geol. Surv.*, Washington, **1106:** 1–37, 8 figs.

—— 1980. Tertiary climates and floristic relationships at high latitudes in the Northern Hemisphere. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **30:** 313–323, 5 figs, 1 tab.

Wolff, R. G. 1975. Sampling and sample size in ecological analyses of fossil mammals. *Paleobiology*, Chicago, **1:** 195–204, 5 figs, 1 tab.

Wood, A. E. 1959. Rodentia. *In* McGrew, P. O., The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. *Bull. Am. Mus. nat. Hist.*, New York, **117:** 157–169, figs 14–27, tabs 7–9.

—— 1962. The Early Tertiary Rodents of the Family Paramyidae. *Trans. Am. phil. Soc.*, Philadelphia, (NS) **52:** 1–261.

—— 1970. The European Eocene Paramyid Rodent, *Plesiarctomys*. *Verh. naturf. Ges. Basel*, **80:** (2): 237–278, 15 figs, 5 tabs.

—— 1976*a*. The Paramyid Rodent *Ailuravus* from the Middle and late Eocene of Europe, and its relationships. *Palaeovertebrata*, Montpellier, **7:** 118–149, 6 figs, 2 tabs.

—— 1976*b*. The Oligocene rodents *Ischyromys* and *Titanotheriomys* and the content of the Family Ischyromyidae. *In* Churcher, C. S. (ed.), *Athlon. Essays in Palaeontology in honour of Loris Shano Russell*: 244–277, 9 figs. Toronto, R. Ontario Mus. Life Sci. Misc. Publs.

—— 1980. The Oligocene rodents of North America. *Trans. Am. phil. Soc.*, Philadelphia, **70** (5): 1–68, 1 tab.

—— **& Patterson, B.** 1970. Relationships among hystricognathous and hystricomorphous rodents. *Mammalia*, Paris, **34** (4): 628–639.

—— **& Wilson, R. W.** 1936. A suggested nomenclature for the cusps of the cheek teeth of the rodents. *J. Paleont*, Menasha, **10** (5): 338–391.

Wood, S. V. 1844. Record of the discovery of an alligator with several new mammalia in the freshwater strata at Hordwell. *Ann. Mag. nat. Hist.*, London, (1) **14** (92): 349–351.

—— 1846. On the discovery of an Alligator and of several new Mammalia in the Hordwell Cliff, with observations upon the Geological Phenomena of that Locality. *Lond. geol. J.*, **1:** 1–7, pls 1–2.

Woodburne, M. O. & Bernor, R. L. 1980. On superspecific groups of some Old World hipparionine horses. *J. Paleont.*, Tulsa, **54** (6): 1319–1348, 7 figs.

Wortman, J. L. 1901. Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum (contd.) *Am. J. Sci.*, New Haven, (4) **12** (68): 143–154, figs 18–30.

Wright, T. 1851. A stratigraphical account of the section of Hordwell, Beacon and Barton Cliffs, on the coast of Hampshire. *Ann. Mag. nat. Hist.*, London, (2) **7:** 433–446.

Wright, V. P. & Mayall, M. 1981. Organism–sediment interactions in stromatolites: an example from the Upper Triassic of South-West Britain. *In* Monty, C. (ed.), *Phanerozoic Stromatolites*: 74–84, 6 figs. Berlin, Heidelberg, New York.

Wrigley, A. & Davis, A. G. 1937. The occurrence of *Nummulites planulatus* in England with a revised correlation of the strata containing it. *Proc. Geol. Ass.*, London, **48** (2): 203–228, figs 18–20, pls 17–18.

Young, C. C. 1944. Note on the first Eocene mammal from South China. *Am. Mus. Novit.*, New York, **1268:** 1–4, 1 fig.

Zdansky, O. 1930. Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeont. sin.*, Peking, (C) **6** (2): 1–87, 5 pls.

Zeuner, F. E. 1941. The Eocene insects of the Ardtun beds, Isle of Mull, Scotland. *Ann. Mag. nat. Hist.*, London, (11) **7:** 82–100.

Zittel, K. A. v. 1893. *Handbuch der Paläontologie*, **4**. 799 pp. Munich & Leipzig.

Index

New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

- Abbreviations 195
- *Acotherulum* 192, 215, 389–91, 391*, 393, 395, **399–400**, 401*, 402*, 403, 403*, 447
  - *campichii* 215, 398*, **399–400**, 401*, 403, 415, 420–1, 424–5, 427*, 428, 440, 443
  - *pumilum* 399, 402*, 403
  - *quercyi* 391*, 393, 399, 403
  - *saturninum* 393, 395*, 399, 403, 425
  - aff. *saturninum* 393
  - sp. 399
- acritarchs 203
- Adapidae 225–6, 265, 267, 443, 445
- Adapinae 267, 274, 280*, **282**
- *Adapis* 267, 269, 274, 277, 448
  - *laharpei* 277, 423
  - *magnus* 274–5, 277
    - var. *leenhardti* 277–9
  - aff. *magnus* 277–8
  - *parisiensis* 274, 277
  - *stintoni* 274
  - *sudrei* 277, 423
  - cf. *sudrei* 425
- *Adapisorex* 226
  - *gaudryi* 226
- Adapisoricidae 224–6, 228–9, 231, 234, 237
- *Adelomys depereti* 301
  - *(Sciuroides) fontensis* 301
- *Aeluravus* 291
- *Aethomylos* 327
- Afton 205, 429, 430
- *Agerina* 267
- *Agerinia* 267, 269
- Ailuravinae 282–3, 291, 295, 425, 445
- *Ailuravus* 213, 282–3, **291**, 293, 295, 440
  - *macrurus* 291, 293, 295, 443, 445
  - *michauxi* 291, 293
  - *picteti* 291, 293–5, 420, 425
  - *remensis* 291
  - *stehlinschaubi* 213, 287*, 291, 292*, **293–5**, 420–1, 423, 425, 428, 443, 445, 448
  - sp. 295
- Albian 437
- Alès Basin 422, 425
- *Alouatta* 443
- *Alsatia* 267
  - *dunaifi* 271*
- *Alsaticopithecus* 223, 225
- Alum Bay 200, 203–6, 415–16, 419, 426*, 429–30
- *Amphichiromys* 329
- Amphidozotheriinae 239
- *Amphilemur* 223, 225–6, 228–9, 231, 234, 239
  - *eocaenicus* 226, 228, 234, 237, 238*
  - *leemanni* 234, 236, 379
  - sp. 225, 234
- Amphilemuridae 223–5, 228–9, 231, 239, 444
- *Amphiperatherium* 212, **215–16**, 217*, 219, 220*, 442
  - *ambiguum* 216
  - *bastburgense* 216, 221
  - *bourdellense* 216, 422
  - *brabantense* 216
  - *exile* 216
  - *fontense* 212, 216, 217*, 218, **220**, 220*, 422, 442–3
  - *frequens* 216
  - *giselense* 216, 219, 422
  - *goethei* 216, 219, 220*, 221, 422
  - aff. *goethei* 212, **216**, 217*, 218–9, 220*, 422, 443
  - *lamandini* 216, 219–20, 422
  - *maximum* 216
  - *minutum* 216, 219, 422
  - sp. 216, 220
- *Amphirhagatherium* 404
- *Amphorichnus* 435
- anagalids 340
- Anaptomorphinae 226, 247
- *Anathana elliotti* 229
- *Anchilophus* 342, 352–3, 448, 450
  - *depereti* 424
  - *desmarestii* 422–3
  - *dumasii* 423
  - cf. *dumasii* 352
  - *gaudini* 423
- *Anchomomys* 192, 223, 225, 267, 269
  - *grisollensis* 225
  - *latidens* 225
  - *pygmaeus* 225
- Ancodonta 404
- Ancylopoda 374
- *Androconus* 222
- Annonaceae 446
- Anoplotheriidae 382, 409, 447
- Anoplotherioidea 409
- anteaters 438
- *Anthracobunodon* 404
  - *louisi* 404, 424
- Anthracotherioidea 382, 404
- Antoingt Zone 324
- Apatemyidae 327–9, 446, 450
- *Apatemys* 327, 336, 446
- Apatotheria 223, 327, 440, 446
- Apocynaceae 446
- Aquitaine Basin 428
- Archaeoceti 342, 432
- *Archaeonycteris* 243
- *Archygromia durbani* 420
- Arcis-le-Ponsart 239, 295, 375, 422, 429
- Arctocyonidae 222, 339
- *Arctogalidea* 446
- *Areoligera undulata* 427*
- *Areosphaeridium dictyoplokos* 417
  - *multicornutum* 427*
- Argenton 343, 345*, 346
- Argile d'Asse 416
- *Argyrotheca piperipyxis* 432
- *Arisella* 274
- Armissan 445, 450
- Arthropoda 420
- Artiodactyla 225, 376, 377*, 414*, 442–3, 447–8, 450
  - indet. **414**
- *Arvaldus* 240
- ascophorans 420
- asteroids 203
- Aubrelong 2 333–4
- *Aumelasia* 376
- Auvers 416
- Auversian 197, 205, 224, 239, 249, 274, 277, 282, 295, 299, 306, 371, 374–6, 383–4, 399, 409, 415–17, 425, 428–9, 449; lower limit 416
- Avenay 291, 329

- Bach 391*
- Bagshot 415
- Ballard Down Fault 437
- Barnard, P. 435
- Barton, Barton Cliff *passim*, esp. **199–207**
  - Beds 199–200, 205–6, 415–17, 430, 432
  - Clay 192, 197, 199–200, 201*, 202*, 203–5, 207, 242, 242*, 342, 371, 416–18, 426*, 428–30, 439*, 440, 448
    - Formation 196*, 197, 198*, 199, 203–6, 344, 356, 373–5, 392, 416–17, 426*, 429–30, 438
      - Member 206
  - Formation 200, 203, 206
  - Sand 200, 203, 205–6
  - series 200
- Bartonian *passim*, esp. **415–29**; cycle 200
- Basilosauridae 342
- *Basilosaurus* 214, **342**
  - sp. 214, **342**
- *Bassaricyon* 446
- *Batillaria* cf. *calcitrapoides* 437
- *Bdeogale* 446
- Beacon Bunny Beds 205
  - Cliff 199, 205–6
- Beauchamp 416
- Becton Bunny 199, 205; Beds 206
  - member 205
  - Sand Formation 196*, 197, 199, 201*, 202*, 203, 205–7, 415–17, 426*, 430, 439*
    - Member 206
- Belgium 325*
- Bembridge 361, 362*
  - Limestone 207, 240, 419, 435–6
  - Marls 361, 433
- *Bembridgia* 210
  - *cincta* 420
- Bernloch 1A 326, 1B 327
- Berville 421–2, 429, 449*
- Binstead 413
- Blackwell, Paddy 342
- Blashenwell 436
- Bond's brickyard 211
- *Bos taurus* 393
- Boscombe Sands 196*, 197, 199, 204, 426*, 429–30
- Bouldnor Cliff 275, 275*
- Bournemouth 342, 429
  - Marine Beds 426*, 430
- Bouxwiller 216, 220*, 252*, 271*, 273, 287*, 329, 334, 340, 341*, 374, 379
- Bovey Basin 437
- Bracklesham 204, 415
  - Beds 197, 200, 204, 416
  - Group 196*, 204, 206, 438
- Braconnac 376
- Bransgore 205
- brick clay 211
- Brockenhurst 206
  - Bed 417
- Buchsweiler 267
- Buff marl 210
- *Bulimus ellipticus* 435
- Burgmagerbein 2 327
- *Buxobune* 376
- *Buxolestes* 444
  - *piscator* 443

- *Cadurceryx* sp. 420
- *Caenopithecus* 267, 274, 444–5
  - sp. 270
- caillasses 416
- Calcaire à *Potamides aporoschema* 426*
  - de Champigny 426*
  - de Ducy 375, 417, 426*
  - de Fons 220, 330, 422
  - de St Ouen 256, 417, 422, 425, 426*, 427, 429
  - Grossier 374, 382, 416, 420, 426*
- calcretes 436
- *Calliostoma nodulosum* 432
- Camelidae 443

canid 446
Capulus 203
Carnivora 212, 327, 336, 338, 438, 442–3
Castrais 288, 428
Castres 288
Catodontherium 410, 450
  paquieri 424
  robiacense 424
Caylux 359*, 391*, 398*, 399, 401*
Cebochoeridae 352, 382, 389–90, 393, 395, 400, 402–4, 415, 447
Cebochoerus 192, 215, 352, **389–93**, 391–2*, 395, 398–400, 401*, 402–3, 402–3*, 447
  anceps 390
  campichii 399
  cf. *campichii* 400
  dawsoni 402
  fontensis 390–1, 391*, 393, 402–3, 402*
  aff. *fontensis* 390–1, 391*, 393, 397
  helveticus 390–1, 391–2*, 393, 395, 397, 398*
  jaegeri 402
  lacustris 390–1, 392*, 393, 395, 397, 398*, 402–3, 402*
  minor 215, **390–1**, 391–2*, 393, 394*, 395, 395–6*, 397, 398*, 399, 402–3, 402*, 424
  robiacensis 215, 390, 391*, 393, **398–400**, 398*, 401*, 402–3, 402*, 415, 420, 424, 443
  ruetimeyeri 390, 399, 402–3, 402*, 420–1, 427*
  cf. *ruetimeyeri* 398
  suillus 399, 402
  sp. 391
  (Gervachoerus) 390, 399
Cenomanian 437
Cercamonius 267, 269
Cercocebus albigena 443
cercopithecid 226, 447
Cercopithecus pogonias 443
cervid 447
Cetacea 212, 342
Chalk 436
Chama Bed 204–7, 432
Chama squamosa 432
Chamblon 344
Characoidei 420, 433, 434*
Chardinyus 329
  sp. 331
charophytes 417, 425, 427–8, 427*, 436
Chasmotherium cartieri 424–5
Chattian 339, 376
Chelonia 420, 433
Cherry Marl 212
Chewton Bunny 198*, 199, 342, 392
Chironomidae 433, 434*
  larval tubes 420, 435
Chiroptera 241, 243
Choeromorus 352, 389–90
  helveticus 352
  jurensis 352
Choeropotamidae 404, 409
Choeropotamus 215, **409**
  depereti 427*
  lautricensis 409, 424, 427*
  sudrei 427*
  sp. 215, **409**, 443
Chorlakkia 376
Christchurch Bay 199–200, 201–2*, 203, 205–6, 417, 430, 437, 439*
chrysochlorids 223
Church Knowle 364
cladogram 269*, 402*
Clasby, Mr & Mrs Paul 342, 392
Clausilia 420
Cochlostoma heterostoma 420
Coelodonta 447
Collinson, M. E. 270, 448
Columbomyinae 296
concurrent range zones 419–20
Condé-en-Brie 291
Condylarthra 212, 222, 327, 338, 340, 371
Cooper, J. 340
Coptostylus 435–6
  brevis 420, 435
coral 427*
Cordieria semicostata 432
correlation 415, 418
cranium 228
Cranston, P. 435
Crassatella tenuisulcata 432
Creech 364
Creechbarrow, *passim*, esp. **207–12**
  Bed 12 210
  Hill 207, 432
  Limestone 193, 207, 212, 240, 371, 428–9, 433, 436–7, 442, 448; Formation, *passim*
creodonts 327, 340, 442
Cresnes 422, 426*
Cretaceous 210
cricetid 298–9
Crocodilia 420, 433, 434*, 440
Crossarchus 446
crustaceans 203
Cryptadapis 267, 269, 274
cryptalgal structures 433
Cryptopithecus 222
  major 223, 223*
  sideroolithicus 223
Cuis 329
Curtis, R. J. 356
Cyanophyta 420, 433–37
cyclothems 206
Cynohyaenodon cayluxi 423
Cytheretta cellulosa 427*

Dacrytheriinae 410
Dacrytherium 215, 406*, **410**, 412*, 447
  cayluxi 410
  elegans 215, 406*, **410**, 412*, 424, 440, 443
  cf. *elegans* 410, 412
  ovinum 410, 412, 412*
  priscum 410
  saturnini 410, 412*
  sp. 410, 412*
Dactylopsila 443, 446
Daniels, I.C. 373
Daubentonia 443, 446
Dendrogale melanura 229
Dendrohyrax 443
dental analogues 443
  nomenclature 222*, 296*, 343*, 377*
depositional environments 430
diacodexids 415
Dibden 196*
Dicerorhinus 447
Dichobune 376
  Campichii 400
  langi 381
  leporina 347
  robertiana 420–1, 427*
  spinifera 376
  sp. 225
Dichobunidae 225, 376, 381–2, 415, 447
Dichobunoidea 376, 402, 404
Dichobunus 419
  leporinus 347
Dichodon 215, 411*, **412–14**, 447
  cartieri 412
  cervinus 412–14, 424
  cf. *cervinus* 215, 411*, **413–14**, 443
  cuspidatus 412–14
  frohnstettensis 412
  lugdunensis 412
  ruetimeyeri 412
  simplex 412
  stehlini 412–13
  subtilis 412, 424
  sp. 215, 411*, **413–14**, 443
Dictulumus 419
  leporinus 347
Didelphidae 215, 442
Didelphinae, Didelphini 215, 443
Didelphis 215
Didelphoidea 215
diet 442
dinocerates 340
dinocysts 203, 416–18, 429, 432
Donrussellia 267, 269
Dormaal 338
Dorset Pipe Clay series 207, 426*
Dorudontidae 342
Dulcidon 339

Ebro Basin 436
Echinosorex 229
  gymnurus 229
Eclépens 290, 309, 310–11*, 350, 409, 449*
  A 290, 428
  B 238*, 239, 256*, 290, 301, 306, 308–9, 311, 412*, 426, 426*, 450
Eclépens-Gare 288, 290, 293, 300–1, 324, 345*, 346–7, 350–2, 400, 410, 412*, 414, 421–2, 424, 426*, 428–9, 442, 449*
École des Mines 344
Ectinochilus planum 427*
Egerkingen 239, 249, 267, 273, 291, 311, 344, 345*, 346–7, 352, 356*, 375, 381, 382*, 383, 385, 389, 409, 412, 418, 422, 425, 426*
  α 275*, 277, 344, 347, 373, 375, 383, 402, 421, 425, 429
  β 402, 421, 424–5, 429
  γ 271*, 299, 344, 370–1, 383, 385, 388–9, 420–1
Ehingen 1 324, 327
  12 326
Ehrenstein 275–6*
  1A 259, 263, 275, 278, 303, 307, 323–4, 327
  1B 326–7
Elfomys 448
  tobieni 423
Elmore 194, 196*, **197**, 199, 203–5, 212, 344, 346, 372*, 374–6, 418, 430
  Formation 196*, 197, 204–6
  Member 199, 344, 374–5, 416–17, 430, 432
England 325*, 429
English China Clays 210–11, 234
Entreroches 260*, 264, 288, 324, 327, 376, 378–9, 409, 414, 450
eocaenum-rhinocerodes Zone 422, 425, 429
Eochiromys 327
Eomoropidae 374
Equidae 361–2, 371
Equoidea 342, 361
Equus 361, 443
Erinaceidae 223–5, 228, 443
erinaceoid 225, 229
Erinaceomorpha 223–4, 228
erinaceotans 226
Erinaceus europaeus 227*, 228
Escamps 450
Estellomys 296–7
Estes, R. 419
Eupleres 446
Europolemur 192, 213, **267**, 270, 271*, 273–4, 444
  collinsonae 192, 213, 267, **270**, 271–2*, 273–4, 423, 443–5
  klatti 267, 270, 271*, 273
  aff. *klatti* 267, 271*, 273
Eutheria 212, 222, 340
Euzet 259, 275–6*, 277, 347, 390–1, 391*, 393, 412*, 415
Exilisciurus 445

faunal composition 440
  provinces 448
Fawley 196*, 205–6, 432; Transmission Tunnel 206
Ferungulata 443
Filholia elliptica 419
  laevolonga 420
Florida Everglades 433, 436
Fluvio-marine series 200, 210, 241, 259, 429
Fonliasmes 421, 429
Fons 422, 425, 426*
  1 301, 350, 425
  2 425
  3 425
  4 220–1, 220*, 315, 391*, 412*, 425, 450
  5 412*, 425
  6 392*, 397, 398*, 425
  7 425
foraminifera 203, 416, 430, 432; agglutinated 432
Ford, R. L. E. 275
Formation de Mortefontaine 426*
France 429
Freshney, E. 206
Friar's Cliff 203, 430

galericines 228–9, 444
Galerix exilis 226
Gardner, R. 228, 256, 370
Gardonyus 329
gastropods 203, 209–10, 419, 427*, 432–3, 436–7, 447; see slugs, snails etc.
Gehlbergschichten 375
Geiseltal 238*, 252–3*, 267, 273, 339, 435
Gentilly 345*
Germany 325*
Gervachoerus 390–1, 399, 402
  campichii 391
  fontensis 391
  minor 397
Gesneropithex 192, 213, **223–6**, 228–9, 230*, 231, 234, 238*, 239, 444
  figularis 192, 213, 224, 226, 227*, 230*, 232–3*, **234–5**, 238*, 239, 423, 440, 443–4
  grisollensis 224, 234, 236–7, 238*, 239, 423, 450
  aff. *grisollensis* 226, 227*, 228, 230*, 236, 238*, 239
  latidens 224, 228–9, 230*, 234, 236, 238*, 239
  peyeri 224–6, 228, 234, 238*, 239
  sp. 224–5, 234, 238*, 239, 423
Glans oblonga 432
Gliravus 426, 448, 450
  robiacensis 423, 425
  aff. *robiacensis* 425–6
glirids 445
gnaw marks 434*
Gösgen Pumpstation 224, 238*
Grande Coupure 275, 324, 326, 446
Grauves 329
Grès de Brenne 429
Grisolles 219, 236, 238*, 256–9, 256*, 260*, 261, 263–5, 270*, 297, 404, 421, 424–6, 428–9, 449*
Gunville 205
Gypse 415

habitat 442
habits 442
Hampshire Basin 196*, 425, 431*, 439*; sedimentation 429
Hamstead Beds 433, 437
Hapalemur 443, 445
Haplobunodon 215, **404–5**, 406*, 407–8, 407*, 411*, 448
  lydekkeri 404–5, 407–9, 407*
  muelleri 404–5, 409
  ruetimeyeri 404
  solodurense 404–5, 407–9, 420–1, 424
  venatorum 192, 215, **404**, 405, 406–7*, 408–9, 408*, 411*, 420–1, 424, 428, 440, 443, 447
  aff. *venatorum* 407*, 409
  sp. 404
Haplobunodontidae 404, 447
Haplomeryx 383, 412, 415, 448
  picteti 424
Hartenberger, J.-L. 295
Headon 308, 433
  Beds 199–200, 203, 240, 300, 303, 324, 326–7, 431*
  Hill 240, 260*, 275–6*, 278*, 284*, 287, 415, 436
    Limestone 275
    Sands 200, 203, 206, 415–16
Headonian 419–20, 422
hedgehogs 227*, 228, 444
Heidenheim 421–2, 448, 449*
Helaletidae 425
Helmstedt 375
Hemiacodon 226
Hengistbury 194, **199**, 203–5, 212, 418, 421–2, 429–30, 437, 442, 446, 449*
  Beds 199, 205, 429
  Head 199, 205
Herrlingen 1 326
Heteraulacacysta porosa 417
Heterochiromys 329
Heterohyus 214, **327–9**, 331, 332*, 333–4, 335*, 336, 446
  armatus 328–30, 334
  europaeus 328–30, 334
  gracilis 328–30
  heufelderi 328–30
  morinionensis 192, 214, **328–31**, 332*, 333–4, 335*, 423, 443, 450
  nanus 328–30, 333–4, 335*, 423
  aff. *nanus* 214, **330**, 331, 332*, 333–4, 335*, 443
  quercyi 328–30, 333–4, 336, 450
  sudrei 328–30, 333–4, 335*, 423
  cf. *sudrei* 214, **330**, 332*, 333–4, 335*, 443
  sp. 328–31, **334**
  (Chardinyus) sp. 329, 331
  (Gardonyus) 329
heteromyid 298
High Cliff 204, 429; Sands and Clays 429
Highcliff Sand and Clay 205
  Sands 199, 430
Hinton Admiral 205
hipparionine 362
Hippopotamidae 443
hipposiderid 243, 245
Hobby, Ken 342
Holocene 436
Homalaxis sp. 432
Homotryblium floripes 427*
Hoogbutsel 327
Hordle Cliff 199, 219, 223, 226, 228, 230*, 237, 239, 256–7, 256*, 260*, 261, 263–5, 275, 275–6*, 277–9, 278*, 321, 327, 329, 334, 356*, 364, 364*, 368*, 369–70, 373–4, 404, 407*, 410, 412, 414; Mammal Bed 226, 227*, 238*
Hordwell 415
horseshoe concretions 209
Huerzeleris 267
Huntingbridge 196*, 204–5
  bed(s) 205
  division 196*, 197, 204, 206, 416, 430
  Formation 417
Huppersand 249, 252*, 267, 382*, 383, 421
Hyaenodon heberti 423
Hylomys 228–9
  suillus 229
Hyperdichobune 215, **376**, 379, 381–2
  hammeli 376, 379
  langi 376, 379, 381
  nobilis 376, 379, 381
  spectabilis 376, 378–9
  spinifera 378–9
  sp. 215, **376**, **378–9**, 380*, 381, 386*, 415, 443, 447
Hyracotherium 293, 344, 371
  leporinum 362
  siderolithicum 347

Indraloris 267
Indri 443, 447
indriids 445, 447
insects 420, 435, 437; burrows 433, 434*, 435
Insectivora 212, 223, 225, 229, 339
Iomys 443, 445
Ischyromyidae 282–3
Ischyromys 283
Ischyrotomus 445
  compressidens 291
Isectolophidae 374
Isoptychus 450
  headonensis 422
Issel 343
Issiodoromyinae 296

Jepsenella 327
Jouy 374
Juglandaceae 446
Jumencourt 356*, 365*

Kallo 416
Kemp, D. J. 199, 375
Kisselovia clathrata angulosa 427*
Klikia vectiensis 420
Kochictis 338–9
Kopidodon 338–40, 446
  macrognathus 443

La Bouffie 220*, 221, 329–30, 382
La Débruge 264, 356*, 364, 365*, 371, 390, 399, 413
La Guittardie 424, 449*
La Livinière 429
La Millette 288
Labidolemur 327
Lacertilia 419–20
Lacey's Farm Quarry 275, 275*, 324, 326–7
Laguarrès 429
Lamandine 390–1, 391–2*, 393, 394*, 395, 396*, 397, 398*, 410, 412*
Lantianius 376
Latilly 429, 449*
Lauraceae 446
Lautrec 376, 398*, 399, 429
lautricense-siderolithicum Zone 422, 425–7
Lavergne 221
Le Bretou 256*, 392*, 397, 398*, 421, 424–5, 428–9, 449*
Le Castrais 421, 424, 428–9, 449*
Le Guépelle 418, 421–2, 428–9
Le Quercy 382
Lee-on-Solent 197, 199, 374–5
Lemuriformes 267, 445
Lemuroidea 443, 446
Leonhardt Mine 267
Leptacodon 239
Leptacotherulum 399
  cadurcense 393, 395*, 399
Leptadapis 213, 267, 269, **274–5**, 275–6*, 277–9, 278*, 282
  capellae 274
  magnus 274–5, 275*, 277–9, 278*, 282, 423, 445, 450
    var. *leenhardti* 277, 282
  aff. *magnus* 213, **278–9**, 278*, 280–1*, 443, 445
  priscus 274, 277

Leptadapis–(continued)
  ruetimeyeri 274, 275–6*, 277, 279, 282
  stintoni 274–5, 275–6*, 277–8, 278*, 282
Leptolophus 343, 425, 428, 448
  nouleti 424, 428
  stehlini 420–1, 424–5, 428
Leptotheridium 410
  lugeoni 424
  traguloides 424
Leptotomus bridgerensis 291
  costilloi 291
  grandis 291
  huerfanensis 291
  leptodus 291
  mytonensis 291
  parvus 291
  sciuroides 291
Les Pradigues 221
Lignite Bed 200, 206, 275
Ligurian 415
Lipotyphla 223–4, 228–9, 340, 379, 444
Lissieu 249, 252*, 299, 306, 345*, 346, 379, 381, 382*, 383, 418, 421, 429
Litolestes 231, 237
London Basin 196*
  Clay 199–200, 429
Long Bank 199
Long Mead End 205; Sands 206
Lophiaspis 374
Lophiobunodon 404
Lophiodon 214, 343, 372*, **374–6**, 422, 447
  buchsowillanum 374
  compactus 374
  cuvieri 374–6, 420, 422, 425
  cf. *cuvieri* 214, 372*, **374–5**
  isselense 374–5
  lautricense 374, 376, 420–2, 424–5, 427*, 442, 446, 448, 449*
  cf. *lautricense* 214, **376**, 422, 425, 442
  leptorhynchum 374
  parisiense 374–5, 420
  remensis 374
  rhinocerodes 374, 420–2, 427*, 429
  sardus 374
  tapiroides 375, 424
  tapirotherium 374
  thomasi 374–5, 420, 422, 424–5
Lophiodontidae 374, 425, 450
Lophiotherium 214, 332*, 342, **347**, 350, 352–3, 390, 419
  atavum 347
  cervulum 347, 350–3, 425, 427*
  aff. *cervulum* 350
  geiseltalensis 347
  magnum 347
  progressum 347
  pygmaeum 347, 350–2, 420–1, 424, 427*
  robiacense 345*, 347, 350–2
  siderolithicum 214, 332*, 345*, **347**. 350, 352–3, 354–5*, 420–5, 427*, 428, 440, 443, 446, 448, 449*
  transiens 347
  voigti 347
Lower Bagshot Beds 207, 419
Lower Brown Coal 267
Lower Calcaire de Fons 288
Lower Freshwater Formation 206
Lower Hamstead Beds 275
Lower Headon Beds 199–200, 206–7, 219, 257, 260*, 261, 275, 277, 287, 404, 410, 412, 414, 417, 426*, 432, 450
Ludian 192, 199, 205, 207, 212, 219–21, 224, 239–40, 246, 252, 256–9, 263, 267, 274, 278–9, 283, 290, 300–1, 307–8, 311, 315, 322–4, 329–30, 339, 343, 347, 350, 370–1, 373, 376, 382, 384, 390–1, 399, 403–4, 409–10, 412–15, 417, 419, 422, 425, 446, 448, 450
Lutetian 216, 219, 224, 239, 249, 267, 274, 282, 291, 295, 297–9, 311, 329, 339, 342–4, 347, 353, 370–1, 373–6, 382, 384, 390, 403–4, 409–10, 412–13, 415–16, 418–20, 425, 429, 438, 440, 442–3, 445, 447
Lymnaea cf. *longiscata* 420
Lymnaeidae 436

Macrocranion 228–9, 231
  tupaiodon 226, 229
Mahgarita 267, 269
Malpérié 329–31, 335*
Mammal Bed 239, 256, 256*, 321, 370
Manitsha 283, 445
Manitshinae 282–3, 284*, **290**, 442–3, 445
Manitshini 282
Marchwood 196*, 205
Margarita 267
Marinesian 197, 205, 219–20, 249, 252, 257–8, 264, 278–9, 282, 288, 290, 295, 300, 307–8, 315, 329–30, 339, 347, 350, 373–4, 376, 384, 391, 398–400, 404, 409–10, 413–18, 422, 425, 428–9; boundary in England 417
Marls with *Pholadomya ludensis* 416
Marmosa 443
Marnes à *Lucina inornata* 417, 426*
Marnes à *Pholadomya ludensis* 415–17, 426*, 428
Marnes d'Euzet 426*
Marsupialia 215
Marsupicarnivora 215
Masillabune 404, 447
  martini 443
Masillamys krugi 443
Maurimontia 291
  picteti 293
Megachiromyoides 291
Megalocochlea pseudoglobosa 420
Megatarsius 267
Melanopsis 435
  cf. *subfusiformis* 437
Meldimys 282
Meliceritites sp. 420
Mémerlein 330, 392*, 393, 397, 398*
Meniscodon 376
menotyphlan insectivores 229
Mesonychidae 340
Messel 224, 339, 438, 442–4, 446–7; adapid 445
Messelobunodon 376, 415, 447
  schaeferi 443, 447
Metadichobune 399
Metatheria 215
Metriotherium 376
Miacidae 336; indet. 336
Miacinae 336, 337*, **338**, 443
Miacis 214, **336**, 338
  exilis 338
  sp. 214, **336**, 337*, 338, 442–3
Miacoidea 336
Microadapis 267, 269, 274, 282
Microcebus 443–4
Microchiroptera **241**, **243**, 244*, **245**, 428, 443–4
  gen. et sp. indet. 242*
microchoerid 226
Microchoerinae 195, 245–8, 265, 267, 269–70*, 444
Microchoerus 213, 225, 245, 247, 255*, **256–9**, 260*, 261, 263–5, 267, 269, 269–70*, 428, 444, 448, 450; Bed 240
  creechbarrowensis 192, 213, 257–8, 260*, **261**, 263–5, 266*, 268, 423, 428, 443
  edwardsi 257–9, 260*, 261, 263–5, 268, 444
  erinaceus 257–9, 260*, 261, 263–5, 268
    edwardsi 259
    erinaceus 259
  ornatus 257–9, 260*, 263–4
  wardi 192, 213, 255*, **257–9**, 260*, 261, 262*, 263–5, 268, 423, 428, 443
  sp. 257–8, 261, 264–5, 268, 270*, 423
Microsuevosciurus 315
microsyopid 225
Microtubus 435
Mid-Dorset Swell 437–8
Middle Headon Beds 199, 417, 426*
Milford-on-sea 199
Milner, A. C. 419
Miocene 216, 267
Mixtotheriidae 381
Mixtotherium 215, 379, **381**, 382*, 383, 388–9, 447
  cuspidatum 381–2, 384, 388–9
  depressum 381–2
  gresslyi 381–3, 382*, 385, 388–9, 424
  aff. *gresslyi* 215, 382*, **383–4**, 386–7*, 388, 443
  cf. *gresslyi* 382
  infans 381–4, 382*, 389, 424
  leenhardti 381–3
  priscum 381–3, 382*, 389
  cf. *priscum* 382–3
  quercyi 381–2
  sp. 215, 386*, **389**, 442–3
Moiachoerus 389, 399
Monera 420
Mont St Martin, Formation de 416
Montmartre 353, 371, 418
Moraceae 446
Mormont 284, 284*, 287–90, 338, 344, 346–7, 350, 352, 378, 382–3, 382*, 388–9, 391–2*, 398*, 399–400, 407, 407*, 409, 414, 448
Mortefontaine 420*
Mouillacitherium 239, 376
  aff. *elegans* 225
  cf. *elegans* 378
Mudeford 203
Mull, Isle of 435
Mutigny 329, 336
Myrtaceae 446

Naish Estate 373
Nannopithex 192, 213, 245, 247, **249**, 250*, 251–2, 252–5*, 257, 265, 267–9, 269*, 444, 448; fold 222*, 231
  filholi 249, 251, 252*, 267–8, 269*
  pollicaris 249, 251
  quaylei 192, 213, **249**, 250*, 251, 252–5*, 268, 269*, 423, 443
  raabi 249, 251, 252–3*, 268, 269*
  sp. 213, 249, 250*, **251**, 252–4*, 423, 443–4
Nasua 446
Necrolemur 245, 257–9, 265, 267, 269, 269–70*, 444, 448
  antiquus 258, 268, 270*
  filholi 249
  parvulus 252
  zitteli 258, 268, 270*, 423
  cf. *zitteli* 268
Necrolemurinae 245
Necrosorex 329
Neomatronella 231
Neotetracus 228–9, 443–4
  sinensis 229
niveaux repères 418, 425
Nogent-l'Artaud 422
Nordshausen bei Kassel 256*
Nummulites 416, 427*, 429
Nummulites prestwichianus 197, 200, 202*, 203–4, 417–18, 427, 432
  rectus 204, 427, 432
  variolarius 206, 416

Nyctitheriidae 224, 239, 241, 444
Nyctitheriinae 239
Nyctitherium 239

Obergösgen 371
Oligocene 216, 219, 239, 315, 327, 336, 436–7, 445, 450
Oltinomyinae 296
Oltinomys 297
Omomyidae 245, 246–7, 267, 269*, 444
Omomyinae 247
Omomyoidea indet. 241
Omomys 226, 247
oncoliths 209–10, 433, 434*, 435–7
Oodectes 336
Ophidia 419–20
Ophiomorpha 205, 207, 430, 432
Opsiclaenodon 222
Örlinger Tal 315
Osborne Beds 275, 308, 324, 413, 433, 436
ostracods 203, 417, 427*, 436
Otocyon 446

Pachynolophus 342
  lavocati 362, 370
  livinierensis 362, 370
Palaearctonyx 336
Palaechthon 225, 228
  nacimienti 229
Palaeocene 216, 222, 239, 327, 435
Palaeochiropterygoidea 243
Palaeodonta 376
palaeoecology 430, 438
palaeoenvironments 430
palaeogeography 430, 448
Palaeoglandina costellata 420
Palaeomarmota 291
Palaeophyllophora 243
palaeoryctids 327
palaeoryctoids 340
Palaeotheriidae 342, 343*, 353, 371, 446, 450
palaeotherioid 352–3
Palaeotherium 214, 342, 353, 357, 361, 364, **371**, 372*, 373–4, 419, 446, 448
  castrense 371, 373–4
    castrense 424
    robiacense 424, 427–8, 427*
  crassum 371, 373
  crusafonti 371
  curtum 371, 373
  duvalii 371
  eocaenum 371, 420–2, 424, 427*
  isselanum 343
  lautricense 371, 420–1, 424
  magnum 371, 373
    stehlini 374
  medium 371, 373
  minus 353
  muehlbergi 371, 373, 424
    praecursum 373
  aff. *?muehlbergi* 214, **371**, 372*
  pomeli 371, 373, 424
  renevieri 371, 373
  ruetimeyeri 371, 373, 424
  ruetimeyeri 373, 429
  siderolithicum 371, 424
  tapiroides 374
  sp. 214, 371, 372*, **373**
Palaeoxestina occlusa 420
Palenochtha 228
Paleomoropus 374
Paloplotherium 353, 361
Paludestrina sp. 437
pangolins 438
Panopea 432
Pantolestidae **222**, 223*, 433, 443–4
Pantomimus 222
Paracyathus 427*
Paradapis 274
Paradelomys 297–301, 448
  crusafonti 297, 301, 423
  depereti 297, 300–1
  quercyi 297
  spelaeus 297
Paralophiodon 374
Paralophiodontinae 374
Paramyidae 282–3, 286*, 291, 292*, 295, 298, 445, 450
Paramyinae 282, 295
Paramys delicatior 291
  delicatus 291
  francesi 291
Paraplagiolophus 342, 356*, 365*
  codiciensis 356*, 363–4, 365*
Paraxiphodon 412
  cournovense 424
Pargny 376
Paris 421, 424, 427–9, 449*
  Basin 224, 415–17, 420–1, 425, 428–9, 437
Parisian 415
Paroodectes 336
  feisti 443
Paroxyclaenidae 338, 340–1, 440, 446, 450
Paroxyclaenus 338, 446
Pelycodus 226
Peratherium 215, 442, 448
  bretouense 422
  lavergnense 422
  sudrei 422
  sp. 219
Periconodon 225, 267, 269, 282
Perissodactyla 342, 442, 446
Perrière 256*, 259, 331, 382, 412*
Petaurista 443, 445
phalangerid 446
Pholadomya ludensis 416–17
Pholidocercus 223–5, 228, 234, 444
  hassiacus 443
Pholidota 438
Phosphorites 282, 330
  du Quercy 228, 230*, 252, 274, 278–9, 338, 356*, 361, 363*, 367*, 369, 381, 382*, 395*; see Quercy
Pinna 432
Pivetonia 245, 249, 269*
  isabenae 249, 267
Plagiolophus 214, 343, **353**, 356*, 357, 359–60*, 361–3, 363*, 364–5, 364–5*, 367–8*, 369–71, 425, 428
  annectens 353, 356*, 357–8, 361–5*, 368*, 369, 371, 424, 428, 450
  aff. *annectens* 448
  cartailhaci 353, 356, 358, 361–2, 424, 448
  cartieri 353, 371
  curtisi 192, 214, **353**, 357, 363, 370–1, 428, 432, 446, 448
    creechensis 192, 214, 356*, 358*, **364**, 367, 367–8*, 369, 370*, 371, 424, 427*, 428, 440, 443
    curtisi 214, **356**, 356*, 358–60*, 362–6*, 367, 368*, 369, 371, 424, 427*, 428
  fraasi 353, 356*, 357, 359*, 361–2, 362–3*, 367*, 369–70
  javalii 353
  lugdunensis 353
  minor 356*, 357, 361, 364, 370–1
  sp. 356, 356*, 360*, 364, 371
planktonic foraminiferal zones 415–16
Planorbidae 436
Pleistocene 198*, 210, 216, 447
plesiadapiform 228
Plesiarctomys 213, **282–5**, 287–8, 290–1, 440, 445
  curranti 192, 213, **283–5**, 284*, 286–7*, 287–90, 423, 440, 443, 445
  cf. *curranti* 284*
  gervaisii 283–5, 288–90, 425
  hartenbergeri 283–5, 287–9, 287*
  hurzeleri 213, 283–5, 284*, **287–90**, 292*, 420–1, 423, 425, 443, 445, 448
  savagei 283–4, 287, 289
  spectabilis 283–5, 287, 289, 420
  sp. 287*, 288, 290
Plesidacrytherium 410
Pleurocyon 336
Podogymnura 228–9
  truei 229, 230*
Poitiers 429
Pont d'Assou 274
Pontifactor 239
Poole harbour 429
Potamides aporoschema 426–7*
  cf. *variabilis* 437
Poulner 205–6
Première Masse du Gypse 353, 371
preservation 438
Priabonian 212, 415, 448
Primates 212, 224–6, 228–9, 231, 245, 444, 447–8
procyonids 446
Pronycticebus 267, 269
  sp. 249
Propachynolophus 342
  maldani 344
Propalaeotherium 214, **342–4**, 347, 371, 446
  argentonicum 343
  hassiacum 343, 443
  helveticum 343
  hengyangense 343
  isselanum 343
  messelense 343–4, 443, 446
  parvulum 343–4, 345*, 346, 423, 446
  aff. *parvulum* 214, **343**, 345*, 346, 348–9*, 443, 447
  cf. *parvulum* 343
  rollinati 343
  sinense 343
Propithecus 443, 447
Proserpina cf. *woodwardi* 420
Prosimii 225, 228–9, 231, 245
Protadelomys 298–9
  alsaticus 297, 299
  cartieri 299, 311
  lugdunensis 299, 306–7
Proteutheria 222–3, 327
Prothryptacodon 222
Protoadapis 267, 269–70, 274
  klatti 270
  sp. 270
Protodichobune 376, 415
Protrogomorpha 282–3
Pseudamphimeryx pavloviae 424
  renevieri 424
  schlosseri 420–1
  valdensis 424
Pseudoloris 213, 245, 249, **251–2**, 254*, 256*, 265, 267, 269, 269*, 444
  crusafonti 252, 256, 256*, 268, 269*, 420, 423, 425
  cf. *crusafonti* 213, 254*, **256**, 428, 443
  parvulus 230*, 249, 256, 268, 423, 450
  reguanti 252, 256, 256*
  sp. 249
Pseudolorisinae 245
Pseudoltinomys 425, 448
  mamertensis 423, 425
  sp. 425
Pseudopalaeotherium 343
Pseudoparamyinae 282
Pseudoparamys 282
Pseudorhinolophus 245
  weithoferi 245
Pseudosciuridae 288, 296, 296*, 297–301, 307–8, 317, 320, 445, 448, 450
Pseudosciurinae 296–7
Pseudosciurus 296, 298–9, 308, 448
  suevicus 445
Pteridium aquilinum 208*

Ptilocercus 443–4
  lowi 229
Pugiodens 338–9
  mirus 339
  sp. 340
Purbeck 437; limestone 211
  Isle of 437
Purgatorius 228

Quayle, W. J. 199
Quercimys 296
Quercy 260*, 265, 270*, 275–6*, 288, 382–3, 391, 410
  phosphorites 228, 267, 275, 301, 385; see Phosphorites du Quercy
Quercygale angustidens 423, 450

radiometric dates 418
Ratufa 443, 445
Raynal 274, 278, 278*
Reithroparamys debequensis 291
Remyinae 296
Remys minimus 423, 428
Rhagatherium 404
  sp. 379
Rhenanian 419
Rhine Graben 448–9
Rhinocerolophiodon 374
rhinoceros 447
Rhinolophus sp. 423
Rhombodinium draco 415–7, 427*, 429
  intermedium 417
  porosum 417, 427*
Rigassi, D. 309
Rissoné, A. 301
Robiac 224–5, 234, 238*, 239, 284*, 288–9, 297, 301, 330, 335*, 345*, 347, 350–1, 353, 373, 398–9, 398*, 413, 418, 421, 424–9, 426*, 440, 442, 449*
Robiacina minuta 424, 428
  weidmanni 424
Roc de Lunel 421
Roc de Santa 450
Rodent Bed 238*, 239
Rodentia 212, 282, 287*, 295, 440, 443–5, 448
Ronheim 1 324, 326
Rupelian 212
Russellites 338–40
  simplicidens 340
  sp. 340

Sabellaria 433
Sables à *Batillaria bouei* 295
  d'Auvers 295, 418
  de Beauchamp 417
  de Cresnes 417, 422
  d'Ezanville 417, 426*
  de Monceau 428
  de Mortefontaine 417
  du Castrais 376, 428
  Moyens 416, 420, 422, 426*
San Cugat de Gavadons 256*
Sands above the Hengistbury Beds 206
Saturninia 239, 241, 448
  beata 241, 423
  gracilis 241
  grandis 241, 423
  grisollensis 241, 423
  hartenbergeri 241, 423
  intermedia 423
  mamertensis 422
Scandentia 229
Schelklingen 1 326
sciuravid 298
Sciuridae 445
Sciurognathi 282
Sciuroides 214, **297–301**, 303, 305–7, 315, 425, 445–6
  ehrensteinensis 300, 303, 305–6, 425
  fontensis 301
  intermedius 300–1
  quercyi 300–1
  rissonei 214, 287*, **300–1**, 302*, 303, 305–6, 306–7*, 320, 423, 426, 428, 443, 445
  ruetimeyeri 300–1
  russelli 300–1, 303, 306, 423, 426, 428
  aff. *russelli* 301
  siderolithicus 297, 300–1, 303, 305–6, 423, 425, 428
  aff. *siderolithicus* 301, 306
  sp. 288–9, 305
Sciuroidinae 296–7, 300
Sciurus 445
  ruetimeyeri 301
  siderolithicus 300
Scraeva 213, **239–41**, 444, 448, 450
  hatherwoodensis 240–1
  woodi 240–1
  sp. 213, 240*, **241**, 443
Sea Road Gap 205
Selsey division 197, 199, 204, 206, 416, 432
Sergy 375, 424, 429, 449*
Sidérolithique 309, 400
Siluriformes 420
Simamphicyon helveticus 420–1, 423, 428
Sinclairella 327, 446
Sivaladapis 267
slugs 420, 433; plates 209–10
snails 209, 419, 433, 435; opercula 210
Solen 432
solenodontids 223
soricids 223
Sosis 392*, 397, 398*
Southampton 206
Souvignargues 390, 392*, 398*
Spaniella 338
Sparnacian 216, 267, 338–9
St Loup 347
St Ouen 422; see Calcaire de St Ouen
Stampian 212, 267, 274, 298, 315, 325*, 343, 353, 390, 399, 410, 448
Ste Néboule 410, 412*
Stehlinella 327
Stone Band 207
stromatolites 433, 435–6
structure 212
Stubbington 197
Studley Wood 196*, 204–5
Suevosciurus 192, 195, 214, 298–300, 303, 310, **315**, 316*, 317, 320–3, 325–6*, 327, 445–6, 448, 450
  authodon 192, 214, 309, **315**, 316*, 317, 318*, 319, 321–2, 322–3*, 327, 423, 440, 443, 445
  ehingensis 315, 322–4, 326–7, 326*, 445
  fraasi 315, 321, 323–4, 325*, 326–7, 326*
  minimus 315, 323–4, 325*, 327
  aff. *minimus* 315
  mutabilis 303, 428
  palustris 315, 324, 325*, 326–7
  romani 297, 300–1, 303, 425
  cf. *romani* 428
  russelli 300, 303, 425
  sp. 315, 321, 450
  (*Microsuevosciurus*) 315
  (*Treposciurus*) *mutabilis* 428
  (*Treposciurus*) *romani* 300–1
Suidae 352
suoid artiodactyl 447
superficial deposits 211
Switzerland 325*, 429
Symplocaceae 446
Synaphodus 376

Taddiford Gap 205
talpids 223
Tapirulus 410
  schlosseri 424
Tapocyon 336
Tarnomys 296–9
  quercinus 297
Tarsiidae 225, 246–7, 444
Tarsiiformes 245, 444–5
tarsioids 448
Tarsius 246–9, 248*, 253*, 256, 443–4
  bancanus 246–8, 253*, 445
    borneanus 246–8, 248*
    natunensis 246, 248*
  spectrum 247–8
  syrichta 246–8, 248*, 253*
Taylor, P. D. 419
teeth 195, 229; curation of small 194
Teilhardina 247
tenrecids 223
Terebellum 432
  fusiforme 432
  sopitum 432
Tetonius 247
Thalerimys fordi 427*
  headonensis 422, 427*
Thaumastognathus 404
Theodoxus 437
Theria 215
Theridomyidae 296–7, 299, 446, 450
Theridomyinae 296
Theridomyoidea 295–8
Theridomys euzetensis 425
  varleti 423, 425
Titanotheriomys 283
Tornatellaea simulata 432
Totland Bay 206, 415
Totton 205
Toulouse 376
tragulid 447
Treposciurus 192, 214, 298–301, 303, **307–8**, 310–11, 315, 316*, 327, 445, 448, 450
  helveticus 192, 214, **307–8**, 311
    helveticus 214, **308**, 310–11*
    preecei 214, 299, **308–9**, 310–11*, 313, 314*, 316*, 327, 423, 443, 445
  intermedius 307–11
  mutabilis 303, 307–9, 311, 428
    helveticus 308
    mutabilis 308
  romani 300–1
  sp. 308
Trichoptera 433, 434*, 435
  larval cases 420
Trogopterus 443, 445
Tupaia glis 229
tupaiids 225, 228–9, 444
Turritella 373
  elongata 417
turtles 203, 435
Tylopoda 412

Uintacyon 336
Uintan 267
Ulm 307
Ungulata 212, 231, 443
Unio brightoni 420
unionid 437
Upper Bagshot Beds 196*, 197
Upper Bagshot Sand 206
Upper Headon Beds 277
Urogale cylindrura 229
Utrecht 195

Vassacyon 336
Vepricardium porulosum 432
Vespertiliavus gracilis 423
  wingei 423
  sp. 423
Vincularia 420
Vitis 446
viverrids 446
Viviers 429
Viviparus 435
  angulosus 420
  cf. *lentus* 420

Vulpavoides 192, 214, **338–40**, 341*, 446
  cooperi 192, 214, **339–40**, 341*, 342, 423, 443, 446
  germanica 339–40
  simplicidens 339–40, 341*, 342
Vulpavus 336, 339

Ward, Mr D. J. and Mrs A. 259
Wareham 331
Warwick Slade 206
Weald–Artois Axis; land bridge 449, 449*
Weidenstetten 301, 306, 425
Weidmann, M. 350
Weissenau 216
Weissenburg 2 324
  6 323, 327
  8 256, 256*, 324
Whitecliff Bay 200, 203–6, 429–30, 432
Wight, Isle of 210, 240, 259, 275, 287, 300, 303, 315, 322–4, 410, 413, 419, 433, 438
Woodipora sp. 420

Xenarthra 438
Xiphodon 412, 448
  castrense 420–1, 424, 428
Xiphodontidae 383, 412, 415
Xiphodontoidea 412

Ypresian 207, 246–7, 249, 283, 291, 328–9, 343, 374, 376, 415, 419, 448

Zeuglodon Wanklyni 342
zones, definition 420
Zygorhiza 214, **342**
  wanklyni 214, **342**

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The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

B. H. Gardiner

There are some 25,000 species of acinopterygians, far out-numbering the tetrapods and accounting for over half of all the living species of vertebrates. The Actinopterygii contain such diverse forms as polypterids, sturgeons, paddle fishes, gars, the bowfin and the enormous variety of teleosts. The Devonian actinopterygians described in this monograph stand near the base of the Osteichthyes, a natural group including the coelacanths, lungfishes and tetrapods.

This unique Upper Devonian fish fauna was discovered in 1963 by Mr Harry Toombs of the British Museum (Natural History) while on a collecting trip to Australia. The majority of the material was subsequently collected in 1967 by a joint expedition from the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow.

The discovery of these superbly preserved Devonian palaeoniscids at Gogo, Western Australia, has not only greatly increased our knowledge of the early actinopterygian condition but has also enabled us to appreciate the original osteichthyan plan. In other words, many of the characters of the Gogo palaeoniscids are primitive for all bony fishes, and this in turn allows comparison with the other gnathostome groups. These Devonian species also provide detailed information which illuminates many problems in the structure and evolution of the actinopterygians. This knowledge has permitted a more comprehensive and soundly based account of the history of that group.

The relationships are expressed in a new classification of gnathostomes in which the placoderms are considered to be the sister-group of the osteichthyans, the acanthodians the sister-group of those two and the chondrichthyans the primitive sister-group of other gnathostomes. The Porolepiformes are considered to be the sister-group of the choanates.

Finally the interrelationships of actinopterygians are reviewed and the great range of fossil forms presently included in the Palaeonisciformes discussed.

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